SYSTEMATIC REVIEW OF ENDEMIC SULAWESI SQUIRRELS (RODENTIA, SCIURIDAE), WITH DESCRIPTIONS OF NEW SPECIES OF ASSOCIATED SUCKING LICE (INSECTA, ANOPLURA), AND PHYLOGENETIC AND ZOOGEOGRAPHIC ASSESSMENTS OF SCIURID LICE

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 339, 260 pp., 60 figures, 58 tables
Issued June 11, 2010

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ABSTRACT

Analyses of fur color patterns, morphometric data derived from external, cranial, and dental dimensions, and distributions of collection sites for voucher specimens form the basis for a taxonomic revision of Sulawesi's endemic squirrel fauna. Eight species of tree squirrels in *Rubrisciurus* and *Prosciurillus* and two species of ground squirrels in *Hyosciurus* are recognized. All are diurnal and inhabit primary forest formations. Diet consists of fruit, nuts, seeds, and arthropods. *Rubrisciurus rubriventer*, the largest in body size, forages on the ground and in the lower canopy layer, is found throughout Sulawesi where primary forest persists, and occurs through an altitudinal range embracing tropical lowland evergreen and lower montane rain forests; it is absent from upper montane rain forest. Five species of arboreal squirrels comprise the *Prosciurillus leucomus* group, a cluster of species occupying the upper forest canopy: *P. leucomus*, known only from lowland and montane habitats in the northern peninsula and one offshore island; *P. alstoni*, recorded from lowland tropical evergreen rain forest in the eastern section of Sulawesi's central core, the east-central and southeastern arms, and two southeastern islands; *P. weberi*, represented by a few specimens from the coastal lowlands of the southern core of Sulawesi; *P. topapuensis*, endemic to the western mountain block in Sulawesi's central core and occurring along an altitudinal gradient from lowland evergreen rain forest to upper montane rain forest; and *P. rosenbergii*, the only species of squirrel collected on islands in the Sangihe Archipelago north of the northeastern tip of the northern peninsula. The *Prosciurillus murinus* group contains two species of small body size: *P. murinus*, found throughout Sulawesi and in all forest formations, from the coastal lowlands to mountaintops, and a forager in the lower canopy layers; and *P. abstrusus*, known only from montane forest habitats on Pegunungan Mekongga in the southeastern peninsula. Of two species of ground squirrels, *Hyosciurus heinrichi* occupies montane forest habitats in the western mountain block of Sulawesi's central core. It is altitudinally parapatric to *H. ileile*, which inhabits lowland evergreen and lower montane rain forests in the western mountain block and northeastern lowlands of central Sulawesi, and montane forest on the northern peninsula.

A slightly revised classification of Sciuridae is provided in which a new tribe, Exilisciurini, is proposed for the Bornean and Philippine *Exilisciurus*. Previously published results of morphological and molecular analyses point to *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* as a monophyletic cluster, the Hyosciurina, nested within a larger clade, the Nannosciurini, which along with Exilisciurini n. tribe and Funambulini, comprise the Nannosciurinae, one of the three subfamilies constituting Sciuridae, and one that contains most of the Indomalayan genera. The present diversity of species endemic to Sulawesi was derived from an ancient lineage that crossed a sea barrier from the Sunda Shelf to Sulawesi during the late Miocene.

Eight new species of hoplopleurid sucking lice (Insecta, Anoplura) are described as parasitizing 8 of the 10 species of squirrels endemic to Sulawesi: *Hoplopleura rubrisciuri* from *Rubrisciurus rubriventer*, *Hoplopleura leucomus* from *Prosciurillus leucomus*, *Hoplopleura alstoni* from *Prosciurillus alstoni*, *Hoplopleura topapuensis* from *Prosciurillus topapuensis*, *Hoplopleura murinus* from *Prosciurillus murinus*, *Hoplopleura abstrusus* from *Prosciurillus abstrusus*, *Hoplopleura heinrichi* from *Hyosciurus heinrichi*, and *Hoplopleura ileile* from *Hyosciurus ileile*. Examples of *Prosciurillus weberi* and *P. rosenbergii* were surveyed but no lice were recovered. A phylogenetic analysis based on cladistic principles for six species of Sulawesian squirrel lice for which both sexes were available is presented and the results discussed with respect to host relationships. These new data are incorporated into a discussion covering zoogeography of global sciurid-sucking louse associations, emphasizing the Indomalayan squirrel fauna.

Globally, members of 11 genera of Anoplura parasitize sciurids, a figure far exceeding the number of anopluran genera associated with any other mammalian family. Nine of these (the enderleinellids, *Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, and *Werneckia*; the hoplopleurid, *Paradoxophthirus*; and the polyplacids, *Johnsonpthirus*, *Linognathoides*, and *Neohaematopinus*) are primary parasites of sciurids. The remaining two (the hoplopleurid *Hoplopleura*, and the polyplacid *Polyplax*) include representatives that are acquired (secondary) parasites of sciurids—the majority of species in these two louse genera parasitize other groups of mammals but a small number of species have transferred to squirrel hosts. Sciurid hosts and geographic distributions of these 11 anopluran genera are discussed. Historically, representatives of *Hoplopleura* colonized different sciurid hosts on several separate occasions with one known

species on a North American tree squirrel (*Sciurus*), two described species on North American flying squirrels (*Glaucomys*), two species parasitizing North American species of chipmunks (*Tamias* and *Eutamias*), 14 described species from Indomalayan nannosciurine squirrels (*Callosciurus*, *Tamiops*, *Rubrisciurus*, *Prosciurillus*, *Hyosciurus*, and *Funambulus*), and one species parasitizing a Chinese xerine ground squirrel (*Sciurotamias*). The zoogeography of the seven sciurid-infesting louse genera known from Southeast Asia is discussed using data from nine different countries or regions (China, Taiwan, Thailand, peninsular Malaysia, Sumatra, Java, Borneo, the Philippines, and Sulawesi). A reduction in the number of sciuirid-infesting anopluran genera and species is apparent from mainland northern/western regions to insular southern/eastern regions with members of seven genera and 23 species described from China but only one genus and eight species from Sulawesi. The absence of known species of *Hoplopleura* from Bornean and Javanese squirrels suggests that such a fauna may await discovery on one or both of these islands.

Six of the eight species of *Hoplopleura* found parasitizing species of endemic Sulawesi squirrels were recovered as a monophyletic clade from a phylogenetic analysis employing anatomical structures associated with male and female lice. (Two species of Sulawesi *Hoplopleura* are based on females and nymphs only and were not incorporated into the analysis.) The monophyletic cluster formed by the Sulawesian squirrel lice joined with the monophyletic assemblage containing the three Sulawesi squirrel genera—*Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*—suggest that the ancestral squirrel lineage that arrived in Sulawesi during the late Miocene may have been carrying its unique *Hoplopleura* parasite.

INTRODUCTION

Clouds shrouded the mountain; downslope the first tendrils of evening winds rattled leathery oak and chestnut leaves, carrying to the man on the ridgetop the rich odors of wet earth, decaying leaf litter, and mossy forest from the high summit. "Malleeee...ooooo," the loud, haunting twilight call of the malleo bird bounced from one ridge to the other, shattering the soft sounds of twilight breezes. High in the canopy a squirrel chattered, providing counterpoint to the malleo's ghostly song. The man looked up but saw only a dark gray body attached to a feathery tail bounding through the interlaced branches. A low chucking growl came from the nearby understory and a large red squirrel with a great bushy tail appeared, scattering the leaf litter as it bounded over the ground in front of the man to disappear down the ridge. As he left the ridge, his movement drew a scolding trill from a little nondescript brown squirrel on a nearby chestnut, its rapidly twitching tail matching its verbal aggression, both disproportionate to its small size. Out of the corner of his eye, the man saw another squirrel, disturbed by the noisy pygmy, jump from a decaying stump to the ground and dash into the understory—no more than a dark brown streak. As the sky darkened and day passed into night, the twilight calls of birds and squirrels gave way to the nocturnal scurry of rats and muffled flight of owls.

The place is the western mountain block in the central core of Sulawesi. The canopy squirrel, *Prosciurillus topapuensis*, is endemic to these mountains. The large red tree squirrel, *Rubrisciurus rubriventer*, occurs throughout Sulawesi in lowland and lower montane forests, and the pygmy tree squirrel, *Prosciurillus murinus*, ranges over the entire island in lowland and montane forest habitats except on the southeastern peninsula where it is replaced in the mountains by a different but closely related species. *Hyosciurus ileile*, one of the ground squirrels, is the dark brown streak.

These are four of the 10 species of squirrels endemic to the mainland of Sulawesi, some of its offshore islands, and the Sangihe Archipelago lying north of the northeastern tip of Sulawesi. The Sulawesian large-bodied tree squirrel, *Rubrisciurus rubriventer*, seven species of small-bodied tree squirrels in *Prosciurillus*, and two species of ground squirrels in *Hyosciurus* form a monophyletic cluster defined by morphological traits (Moore, 1959). The same clade has been recovered by analyses of mitochondrial, ribosomal, and

nuclear DNA sequences, a group that likely evolved from a single ancestral lineage that crossed the Makassar Strait from the Sunda Shelf to Sulawesi 11.4 to 10.5 million years ago (Mercer and Roth, 2003).

We studied samples of these squirrels with two major research goals in mind; the results form the core of this report. One inquiry centers on defining species-limits of the Sulawesi endemic squirrels using specimens housed in collections of museums in North America, Europe, and Asia. It is from these voucher specimens that we gathered data concerning color patterns of the fur; qualitative aspects of physical build and cranial conformation; external, cranial, and dental measurements; diet derived from field observations and examining stomach samples; and information associated with collection localities. Supplemental information comes from field journals and publications. We also include ecological observations made by Durden when he worked in the northern peninsula and Musser during the time he worked and lived in central Sulawesi. Results reflect an alpha-level systematic endeavor.

The other goal presents results from surveying skins representing the endemic Sulawesi squirrels for sucking lice (Insecta, Anoplura). We looked not only to broaden knowledge about this parasite fauna in the context of hosts and geographic distributions but to test concordance between species-diversity of hosts with that of parasites. Many groups of sucking lice are host specific and phyletically track their hosts (Kim, 1985, 1988; Light and Hafner, 2007; Smith et al., 2008): "Among insects, no group is more specialized for parasitism than are lice (Phthiraptera) because they are probably the only insect parasites to spend their entire life cycle, from egg to adult, on one host" (Grimaldi and Engel, 2005: 278). Because of this intimate bond between parasite and the parasitized, morphological comparisons among the Anoplura residing on the Sulawesian squirrels would add another set of data potentially useful for discerning species-limits of the hosts.

Collectively, sciurid rodents are parasitized by 11 genera of sucking lice, which far exceed the number of louse genera known to parasitize any other family of mammals (Durden and Musser, 1994). These 11 genera are characteristic ectoparasites of various species of sciurids occurring in different parts of the world. Despite this wide diversity of associated anopluran parasites, the sucking louse faunas of squirrels indigenous to the Indomalayan region are poorly known. A few species have been described from squirrels native to the Sundaic islands of Sumatra, Java, Borneo, and the Philippine island of Palawan, but no lice have been documented from squirrels inhabiting other islands in the Palawan faunal region or in the Mindanao faunal region of the southern Philippines (the only two insular clusters harboring endemic squirrels; Heaney et al., 1998), or east of the Sunda Shelf on Sulawesi (which is, along with the Palawan and Mindanao faunal regions, the easternmost limit of sciurid distribution in the Indomalayan region). Squirrel populations from these islands have either not been sampled for their ectoparasite fauna, or sucking lice failed to accompany the ancestral sciurids to Sulawesi and the southern Philippines when ancestral lineages of these rodents colonized islands east of mainland Southeast Asia and the Sunda Shelf. We show that for Sulawesi, the former scenario is true. Sulawesian nannosciurine squirrels turn out to be parasitized by eight species of Anoplura, none of which has previously been described.

The following pages cover several subjects. We introduce the endemic Sulawesi squirrels by summarizing their phylogenetic position within Sciuridae, present the details supporting our view of their species-diversity and ecological data when available, briefly discuss identities of the two species of squirrels that were collected on Sulawesi but are not native to the island, and expose the gaps in our taxonomic exposition by suggesting future research inquiries. We describe eight new species of Anoplura in the genus *Hoplopleura*, provide a phylogenetic analysis of the Sulawesi squirrel lice, speculate on the mode of historical colonization of Sulawesian squirrels by these parasites, and discuss the phylogenetics and zoogeography of sciurid-sucking louse associations with emphasis on the sciurid louse fauna of the Indomalayan region.

SPECIMENS AND METHODS

The Squirrels

Institutions: The definitions of species of *Rubrisciurus*, *Hyosciurus*, and *Prosciurillus* we document here are determined from study of specimens stored in the following institutions: the American Museum of Natural History, New York (**AMNH**); Academy of Natural Sciences, Philadelphia (**ANSP**); the Natural History Museum, London (**BMNH**); Field Museum of Natural History, Chicago (**FMNH**); Museum Zoologicum Bogoriense, Cibinong, Java (**MZB**; now the Indonesian National Museum of Natural History; also known as the Research Center in Biology-Lembaga Ilmu Pengetahuan Indonesia); Naturhistorisches Museum Basel, Switzerland (**NMB**); Nationaal Natuurhistorisch Museum, Leiden (**RMNH**); Senckenberg Museum, Frankfurt am Main (**SMF**); Staatliches Naturhistorische Sammlungen Dresden, Museum für Tierkunde (**SNSD**); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (**USNM**); Zoological Museum of the University of Amsterdam (**ZMA**); Zoologisches Museum und Instituut für Naturkunde der Humboldt-Universität zu Berlin, Berlin (**ZMB**). Specimens we reference by catalog number in gazetteers, tables, text, and figure legends are preceded by one of these acronyms.

Specimens: For the most part, the voucher specimens consist of standard museum preparations, a stuffed skin and accompanying cranium and mandible, or skin mounted in live pose from which the skull was extracted. Color descriptions for *Prosciurillus leucomus*, *P. weberi*, *P. rosenbergii*, and *P. abstrusus* are derived from those museum specimens—Musser's fieldwork never took him to the geographic regions where those species reside. Color descriptons of *Rubrisciurus rubriventer*, *Prosciurillus alstoni*, *P. topapuensis*, *P. murinus*, and the two species of *Hyosciurus* come from material collected by Musser and from older museum specimens; Musser's field journals (stored in mammalogy archives at AMNH), where he recorded coloration and other details of freshly caught squirrels, were also consulted. Fluid-preserved whole specimens or skinned carcasses were also preserved by Musser in the field where they were initially fixed in 10% formalin, soaked for several days in water, then finally stored in 70% ethanol.

Measurements: Values for external linear dimensions are from two groups of specimens. One consists of samples collected by Musser from forests of Central Sulawesi. For each individual in these lots, he measured total length; length of tail vertebrae (LT), which excluded the long hairs at the end of the tail (descriptions of new species published in the 1800s and early 1900s often included length of tail without the terminal tuft, and length of tail with the terminal spray of hairs); length of hind foot, including claw (LHF); length of ear (LE), from notch to crown, and excluding any distal tuft of hairs. He took these measurements soon after a squirrel was caught, and weighed it at that time to obtain a value for body mass or weight (W, in grams). Values for length of head and body (LHB) employed here were derived by subtracting length of tail vertebrae from total length.

The second group contains specimens in museums caught and prepared by other collectors. They recorded total length, length of tail, length of hind foot, sometimes length of ear, but rarely weight. We used their values for length of tail (tail vertebrae only), length of hind foot and length of ear if present (H.C. Raven, the collector of specimens in USNM, did not measure this dimension), but sometimes with reservations, which are explained in footnotes to relevant tables. We did not use total length if notated on the specimen tags, employing that value only to subtract the value for length of tail from it to obtain an estimate of length of head and body.

In the laboratory, several measurements were made on specimens from both groups. We measured lengths of overfur (LDF) and guard hairs (LGH) on the dorsum near the rump by placing a ruler at a right angle to the skin surface and recording the approximate mark where ends of the bunched hairs rested; the technique is unsophisticated and the results imprecise, but still provide a descriptive estimate of lengths for those pelage constituents.

Using dial calipers graduated to tenths of millimeters, we measured the following cra-

nial and dental dimensions (listed in their order of appearance, as acronyms, in the tables; limits are illustrated in fig. 1):

ONL occipitonasal length (= greatest length of skull; distance from tip of the nasals to posterior margin of the occiput)

CBL condylobasal length (greatest distance from the anterior margin of the premaxillaries to the posterior margins of the occipital condyles)

ZB zygomatic breadth (greatest breadth across the zygomatic arches)

IB interorbital breadth (least distance, as viewed dorsally, across the frontal bones between the orbital fossae)

LN length of nasals (greatest distance from anterior tip of a nasal bone to the posterior margin at the naso-frontal suture)

LR length of rostrum (from tip of a nasal bone to the anteriormost border of the orbit)

BR breadth of rostrum (greatest breadth across ventral surface of the rostrum between ventral margins of the infraorbital foramen)

HR height of rostrum (distance from dorsal surface of the nasals to ventral surface of the premaxillary at the premaxillary-maxillary suture; measured only on *Hyosciurus* skulls)

MB mastoid breadth (greatest breadth across the occiput at levels of the mastoid)

HBC height of braincase (from top of the braincase to the ventral surface of the basisphenoid)

LO length of orbit (distance from the anteriormost margin of orbital fossa to tip of postorbital process)

LD length of diastema (distance from posterior alveolar margins of upper incisors to anterior alveolar margins of third upper premolars)

LBP length of bony palate (distance from posterior edge of incisive foramina to posterior margin of bony palate)

PPL postpalatal length (distance from the posterior margin of the palatal bridge to edge of the basioccipital—ventral lip of foramen magnum)

BBP breadth of bony palate at fourth premolar (distance between labial margins of fourth premolars)

LB length of auditory bulla (greatest length of the bullar capsule, excluding the short and bony eustachian tube)

CLPMM crown length of maxillary cheek teeth (from anterior enamel face of PM4 to posterior enamel face of M3)

LPT length of tube formed by nasals and premaxillaries projecting beyond anterior faces of the incisors (distance from the tip of a nasal bone to the bottom of the premaxillary where it forms the anterior rim of the incisor alveolus; measured on *Hyosciurus* skulls only)

Musser measured the skulls in most samples that are documented in this report. Nearly as many additional specimens were examined by him but the skulls are damaged and were not measured. Except for the specimens Musser collected, which were obtained mostly with Conibear traps (fig. 2), Sulawesi squirrels were collected by shooting with a shotgun and the pellets damaged many skulls, especially those from the small-bodied species, *Prosciurillus murinus* and *P. abstrusus*. Sometimes a full set of measurements, which was required for multivariate analyses of the cranial and dental variables we used, could be obtained from a damaged skull, but unfortunately most of the damaged skulls were unsuitable for our purposes.

Musser also measured skulls of type specimens at the AMNH and USNM. However, we depended on the unselfish efforts of curators in several European and Asian museums for measurements of types held in those institutions.

AGE AND SEX: We separated specimens into one of the following five age groups:

OA old adult, body size among the largest in a sample; adult pelage; cusps on fourth premolar and three molars obliterated or nearly so, the crowns forming shallow basins; basioccipital and basisphenoid completely fused, basisphenoid and presphenoid fused in *Rubrisciurus* and *Hyosciurus* but suture persists in *Prosciurillus*.

A adult, body size among the largest in a sample; adult pelage; occlusal surfaces of premolar and molars retain patterns of major cusps but their enamel margins are worn low, broadly exposing the dentine; basioccipital and basisphenoid completely fused, basisphenoid and presphenoid fused in *Rubrisciurus* and *Hyosciurus* but suture persists in *Prosciurillus*.

YA young adult, body size usually smaller than older adults; fresh adult coat; coronal surfaces of premolar and molars slightly worn; enamel borders of cusps and laminae much higher than the enclosed dentine, which has a restricted exposure; basioccipital and basisphenoid suture completely or partially fused and basisphenoid and presphenoid open in *Rubrisciurus* and *Hyosciurus*, but basioccipital-basisphenoid and basisphenoid-presphenoid sutures open in *Prosciurillus*; both sets of sutures open in very young adult *Hyosciurus*.

J-A juvenile-adult, all cheek teeth erupted, crowns unworn or showing slight wear; mostly in juvenile fur that conceals replacement hairs of partially proliferated adult coat, older animals retain juvenile pelage along back and rump but possess fresh adult fur on venter and sides of body; basioccipital-basisphenoid and basisphenoid-presphenoid sutures open in all genera.

J juvenile, body size among smallest in a sample; full juvenile pelage, which is finer than the adult coat, and usually not as bright; upper and lower third molars unerupted or if erupted usually unworn.

These roughly defined age groups are unequally represented among samples: old adults and juveniles are scarce, adults and young adults are most common. Old adults, adults, and young adults were combined into samples from which measurements were obtained for multivariate analyses and univariate descriptive statistics.

Males and females were not separated in any of the statistical analyses. Inquiry into this aspect of morphological variation within and among species will have to be the subject of future studies.

STATISTICAL ANALYSES: Standard univariate descriptive statistics (mean, standard deviation, and observed range) were calculated for the population samples (identified in table 1) and species listed in the tables.

Cluster analyses provided visual patterns that reflect similarity or contrast in the combination of cranial and dental dimensions among geographic samples of a single species or between samples of two different species. Measurements from complete skulls of adults only (young to old) were used in the analyses (geographic sources of the population samples, and identities of the specimens measured, are listed in table 1). All measurements were transformed to natural logarithms. Principal-components analyses were computed using the combination of cranial and dental variables indicated in various tables throughout the text. Principal components were extracted from a covariance matrix and projected on three axes, but usually significant structure was revealed only in the ordination of first and second principal-components factors, which are illustrated. (The pattern of specimen scores in plots employing first and third principal components were usually similar to those bounded by first and second axes.) SYSTAT 11 for Windows (2004 edition) was used for all analytical procedures.

STOMACH CONTENTS: Musser recorded in his field journal the contents found in stomachs of some freshly caught squirrels. Sometimes only a general description was possible—presence of fruit, seeds, arthro-

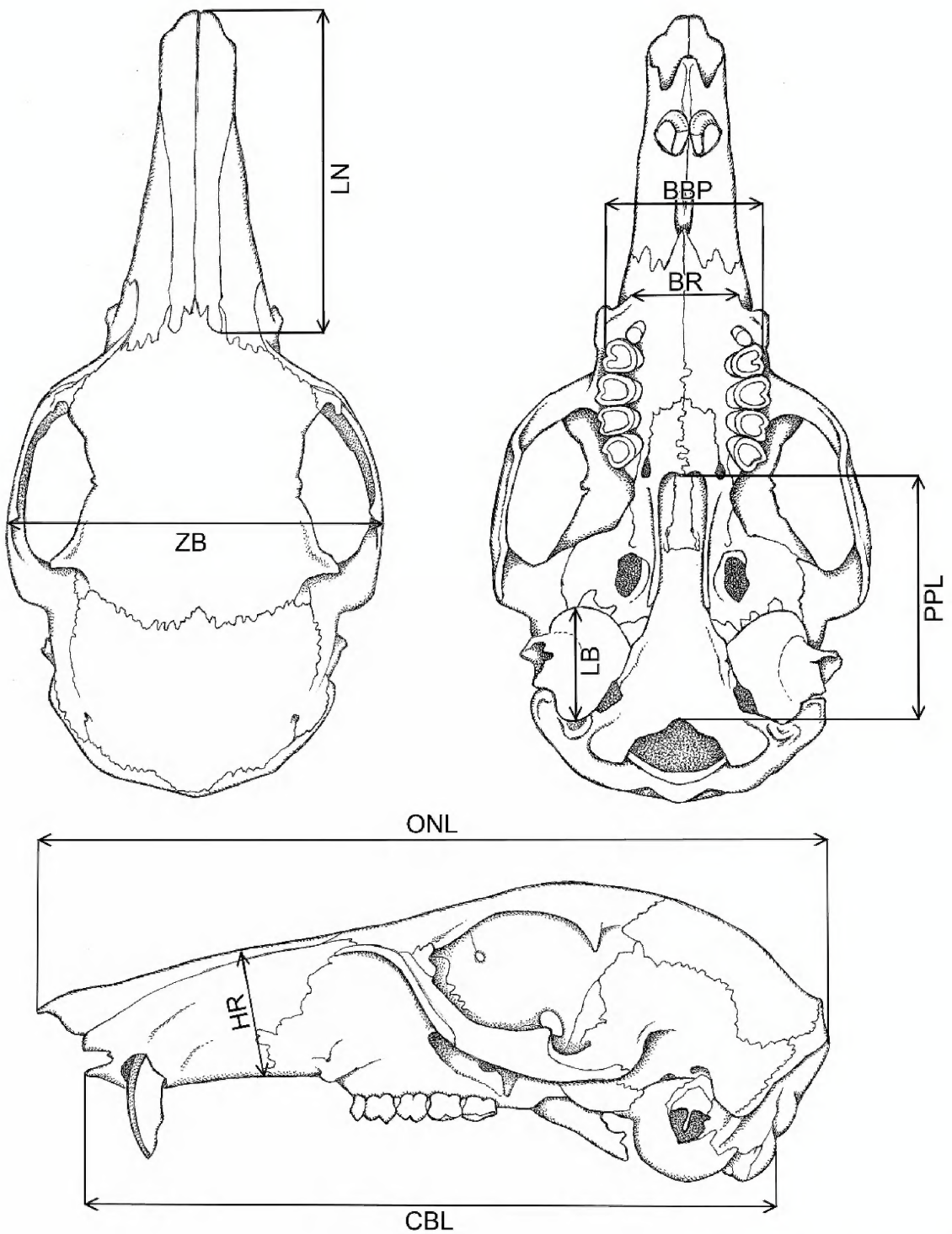

Fig. 1. Diagrams (above and at right) of the cranium of an adult *Hyosciurus heinrichi* showing limits of cranial and dental measurements. Abbreviations are explained in the text.

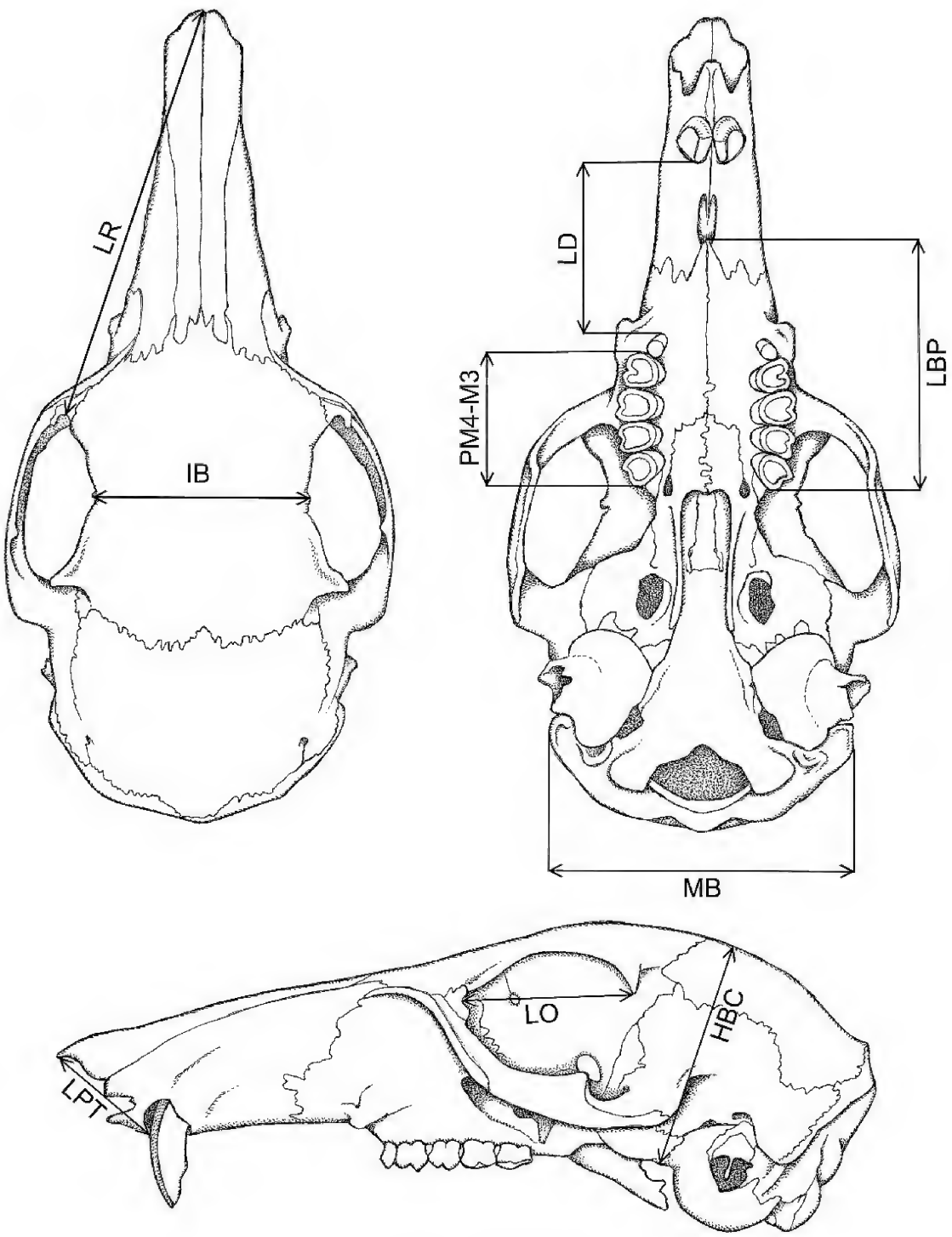

Fig. 1. *Continued.*

Fig. 2. The Conibear (single spring #110) body-gripping trap, which was used by Musser to catch nearly all the squirrels he collected. These traps were baited with a mixture of peanut butter, raisins, oatmeal, and bacon, and set on tree trunks and limbs spanning streams and ravines, in the crowns of understory trees and on large woody vines, on top of rotting tree trunks and limbs lying on the forest floor, and in runways beneath tree trunks and decaying treefalls. Photographed by Darrin P. Lunde.

pods, for example—but often freshly ingested and masticated fruit and seeds could be easily identified by color, shape, and texture as coming from particular trees or vines, and some arthropod remains could be identified to order. Many samples were preserved in ethanol and examined later in the laboratory using a dissecting microscope, which revealed the presence of additional particulates—termites especially—not seen in the field. We supplemented this material by extracting stomachs from undissected squirrels. Stomachs were removed by severing the posterior end of the esophagus and the anterior section of the duodenum. We bisected the isolated stomach along the midfrontal plane, transferred the contents to a white ceramic dish, and examined them with a dissecting microscope. In addition to remains of ingested foods, stomachs contained strands of hair, likely ingested during grooming, and sometimes nematodes. Stomachs emptied in the field are still attached to the gasterointestinal tract of carcasses preserved in fluid at AMNH. Those stomachs extracted in the laboratory are stored, with their contents, in leak-proof vials in the fluid collection at AMNH.

Our survey of stomach contents is far from exhaustive. We did not extract the stomach of every specimen collected, and we did not attempt to identify every tiny insect fragment. We also had no way to determine if any of the tree squirrels included vascular fluids (tree sap or gum) in their diets. We did not detect pieces of fungal remains at the gross level, but this was not conclusive because we did not survey stomach contents for spores or other microscopic evidence of fungi. During his daily work in the forest, Musser looked for squirrel activity, especially squirrels foraging, but this effort was secondary to his primary research centering on an inventory of murid rodents. Unfortunately, squirrels—as opposed to rats and mice—did not usually enter cage-traps (only two animals were caught in these live-traps) so Musser could not supply captives with a range of different forest foods to determine what would be accepted or rejected. The sole exception is described in the account of *Hyosciurus ileile*.

The problem of identifying arthropod remains, particularly insects, found in squirrel stomachs was solved by tapping David Grimaldi's (AMNH) wide-ranging knowledge of insects in particular and arthropods in general. Several times he unselfishly diverted his own research efforts to examine vials containing a range of different arthropods and to provide us with identifications along with ecological insights relating to the animals. His determinations and exposition of habitat preferences provided explicit ecological contexts for the arthropods that usually coincided with Musser's observations of the squirrel's behavior in the forest, and their external and skeletal morphology in the laboratory. We also consulted various general publications covering insects, but found Grimaldi and Engel's (2005) "Evolution of

the Insects" to be the most rewarding, not only for the information it contained in text and illustrations, but for the intellectual satisfaction we derived from learning about different insect groups of interest to us and their evolutionary origins.

GEOGRAPHY: The island of Sulawesi consists of a **central core** from which four arms or peninsulae radiate (see the distribution maps): the **northern peninsula**, which ends in a northeastern jog; the **east-central peninsula**; the **southeastern peninsula**; the **southwestern peninsula**. We use these informal labels when describing distributions of various species of squirrels over the island. Squirrels also occur in Kepulauan Sangihe, the archipelago north of the northeastern tip of Sulawesi's northern peninsula.

In the text and in some tables we refer to the **west-central region** or **western mountain block**, which forms the western portion of Sulawesi's central core. It is that region of foothills, peaks, and interior valleys situated above 100 m and lying roughly west of Danau Poso and extending from the Palu area in the north to Pegunungan Latimojong in the south. For our purposes here it excludes the coastal strip along the shores of the Makassar Strait simply because no nonvolant mammals have been collected there. A suite of mammals, from shrews to rats, have been collected only in the west-central region: a few species are found in tropical lowland evergreen rain forest covering lower altitudes on foothills and in valleys, but most occur at higher altitudes in montane forests.

Throughout the report we use the Indonesian terms **sungai** (stream or small river), **kuala** (stream discharging directly into the sea), **gunung** (mountain), **pegunungan** (mountain range), **pulau** (island), **kepulauan** (archipelago), **selat** (strait), **tanjung** (cape), and **teluk** (bay).

MUSSER'S TRANSECT: During 1973–1976, Musser lived and worked in the forests of central Sulawesi where he focused on an inventory of murid rodents along a transect extending from near sea level into montane habitats. While murids were of primary interest, other small mammals were also trapped, among them reasonable samples of *Rubrisciurus rubriventer*, three species of *Prosciurillus*, and the two species of *Hyosciurus*. These samples proved to be extremely important, in that habitat and other biological information are attached to specimens. Musser's experience with the squirrels where he worked provided ecological insights into habitats and distributions for species occurring in other geographic regions of Sulawesi. In parts of the text, we refer to "Musser's transect" and we provide three maps (figs. 2, 3, and 17) illustrating the location of camps along that transect. Detailed descriptions of the camps and forests will be produced elsewhere (Musser, MS), but we insert the maps here to give readers a visual orientation to the regions surveyed. Ambient air temperatures recorded at the various camps are summarized in table 2; we refer to these data in the descriptions and figures of habitats.

GAZETTEERS: Localities from which samples were collected, along with the institutional initials and catalog number of each specimen examined, are listed in the gazetteers scattered throughout the text in relevant accounts of species. Descriptions of localities and elevations (recorded in meters or feet, depending on the convention used by the collector) were taken from labels attached to skins. These basic data were enhanced where necessary by information from field journals, other archival material, and published expeditionary accounts and gazetteers; sources are cited in the locality entry.

Spelling of locality names are those approved by the United States Board on Geographic Names in the Gazetteer of Indonesia, Third Edition, volumes 1 and 2, published by the Defense Mapping Agency, Washington, D.C. in 1982 (referenced as USBGN, 1982). Some places could not be located in that gazetteer but were found on the topographic map sheets described below; alternate spellings of some place names come from Musser's field journals and older maps.

Coordinates for some collection localities were found in USBGN (1982) or the Gazetteer of Celebes published in 1944 through the Hydrographic Office of the United States Navy Department (HOUSND, 1944). Coordinates for most of H.C. Raven's collection localities were estimated from his personal copy of a Dutch map of Celebes on which he had marked his camp sites and

TABLE 1

Population Samples from Species of *Rubrisciurus*, *Hyosciurus*, and *Prosciurillus* Employed in Analyses of Cranial and Dental Variables

(Specimens measured are identified in footnotes. Localities, along with elevations and geographic coordinates, can be located in the gazetteers and on the distribution maps. Numbers in parentheses for each species indicate total number of specimens measured.)

Species and population sample	*N*	Locality
Rubrisciurus rubriventer[a]	(48)	
Northeastern peninsula	2	Rurukan, Temboan
Northern peninsula	5	Bumbulan, Gunung Ile-Ile
North-central region 1	18	Sungai Miu, Sungai Oha Kecil, Sungai Sadaunta, Tomado, Gunung Kanino, Kulawi
North-central region 2	19	Kuala Navusu, Sungai Tolewonu
Southeastern peninsula	5	Wawo, Masembo, Tanke Salokko
Prosciurillus leucomus[b]	(26)	
Northeastern peninsula	18	Likupang, Teteamoet, Rurukan, Temboan
Northeastern peninsula	8	Sungai Paleleh, Bumbulan, Gunung Ile-Ile, Labuan Sore, Bumbarujaba
Prosciurillus alstoni[c]	(63)	
Malakosa region	32	Kuala Navusu, Sungai Tolewonu
Pinedapa	19	
Southeastern peninsula	11	Wawo, Masembo, Lalolei, Mowewe, Sungai Ahua
North-central region	1	Mapane
Prosciurillus weberi[d]	(5)	
South-central region	5	Masamba, Palopo
Prosciurillus topapuensis[e]	(50)	
Sungai Miu-Sungai Sadaunta	9	
Gunung Kanino	5	
Gunung Lehio	9	
Besoa region	5	Besoa, Lindu Trail
Rano Rano	11	
Pegunungan Latimojong	11	
Prosciurillus rosenbergii[f]	(6)	
Kepulauan Sangihe	6	Pulau Siau, Pulau Tahulandang, Pulau Ruang
Prosciurillus murinus[g]	(57)	
Northeastern peninsula	7	Teteamoet, Gunung Klabat, Temboan
Pulau Lembeh	4	
Northern peninsula	9	Sungai Paleleh, Bumbulan, Gunung Ile-Ile
North-central region 1	18	Sungai Miu, Sungai Oha Kecil, Sungai Sadaunta, Tomado, Gunung Kanino, Kulawi
Gunung Lehio	1	
Rano Rano	2	
North-central region 2	16	Pinedapa, Kuala Navusu, Sungai Tolewonu
Prosciurillus abstrusus[h]	(14)	
Pegunungan Mekongga	14	Tanke Salokko
Hyosciurus ileile[i]	(13)	
Gunung Ile-Ile	2	
Sungai Tolewonu	3	
Sungai Sadaunta	3	
Gunung Kanino	5	

TABLE 1
(Continued)

Species and population sample	*N*	Locality
Hyosciurus heinrichi[j]	(32)	
Gunung Kanino	5	
Gunung Nokilalaki	17	
Pegunungan Latimojong	4	
Pegunungan Takolekaju	6	(= Molengraff range)

[a]Rurukan: AMNH 101324. Temboan: USNM 217824. AMNH 152909, 152910. Gunung Ile-Ile: AMNH 101321, 101322, 196508. Sungai Miu: AMNH 224055, 224056. Sungai Oha Kecil: AMNH 224621–23. Sungai Sadaunta: AMNH 224053, 224624–26, 226839, 226840. Tomado: AMNH 223467, 224057. Kulawi: USNM 218710. Gunung Kanino: AMNH 223552, 225488–90. Kuala Navusu: AMNH 226052, 226053, 226055–60, 226062. Sungai Tolewonu: AMNH 226522, 226526–31, 226533–35. Wawo: AMNH 101314. Masembo: AMNH 101317–19. Tanke Salokko: AMNH 101312.

[b]Likupang: USNM 216786–88, 216791. Teteamoet: USNM 216772–79, 216784, 21685, 216769. Rurukan: AMNH 196571, 196572. Temboan: USNM 217825. Sungai Paleleh: USNM 200270, 200272. Bumbulan: AMNH 152917. Gunung Ile-Ile: AMNH 196560. Labuan Sore: USNM 218075–77. Bumbarujaba: USNM 218709.

[c]Kuala Navusu: AMNH 226076, 226080–85, 226087, 226088, 226090, 226092, 226094–101. Sungai Tolewonu: AMNH 226510, 226511–13, 226516–24. Pinedapa: USNM 219511, 219512, 219515–17, 219520, 219523, 219525, 219527, 219529, 219531–33, 219535–37, 219538–40. Wawo: AMNH 101331, 101332, 101335, 101337, 101339, 101344. Masembo: AMNH 101341, 101343. Lalolei: AMNH 101327. Mowewe: NMB 4243 (lectotype of *Sciurus mowewensis*). Sungai Ahua: NMB 4244 (paralectotype of *Sciurus mowewensis*). Mapane: SNSD B3826 (lectotype of *Sciurus sarasinorum*).

[d]Masamba: MZB 6252, 6253. Palopo: MZB 6254, 6256; RMNH 13342 (lectotype of *Sciurus weberi*).

[e]Sungai Miu: AMNH 224042. Sungai Sadaunta: AMNH 224041, 224581–86, 226835. Gunung Kanino: AMNH 225501–505. Gunung Lehio: USNM 218714–18, 218720–23. Besoa: USNM 219485, 219488, 219489, 219502. Lindu Trail: USNM 218719. Rano Rano: USNM 219483, 219484, 219486, 219487, 219491, 219492, 219495, 219498, 219499, 219501, 219503. Pegunungan Latimojong: AMNH 196534–41, 196544–46.

[f]Pulau Siau: RMNH 13362 (lectotype of *Sciurus rosenbergii*). Pulau Tahulandang: SNSD B2842 (lectotype of *Sciurus tingahi*), B2843 and B2844 (paralectotypes of *Sciurus tingahi*). Pulau Ruang: SNSD B2850 and B2851 (paralectotypes of *Sciurus tingahi*).

[g]Teteamoet: USNM 216793, 216794. Gunung Klabat: USNM 217809. Temboan: USNM 217818–20. Pulau Lembeh: USNM 217810, 217812, 217813, 217814 (holotype of *Sciurus evidens*). Sungai Paleleh: USNM 200276, 200278. Bumbulan: AMNH 152932, 152938, 152940, 152943. Gunung Ile-Ile: AMNH 196520, 196524, 196525. Sungai Miu: AMNH 224046, 224049. Sungai Oha Kecil: AMNH 224591–95. Sungai Sadaunta: AMNH 224044, 224045, 224596–224598, 224600, 226837. Tomado: AMNH 224050. Gunung Kanino: AMNH 225492, 225496. Kulawi: USNM 218713. Gunung Lehio: USNM 218712 (holotype of *Sciurus murinus necopinus*). Rano Rano: USNM 219508, 219510. Pinedapa: USNM 219504, 219505, 219507. Kuala Navusu: AMNH 226064–66, 226070, 226071, 226075. Sungai Tolewonu: AMNH 226500, 226502, 226504, 226506–509.

[h]Tanke Salokko: AMNH 101354, 101356, 101358, 101359, 101361, 101364–68, 101372, 101375, 101376, 101378 (holotype of *Prosciurillus abstrusus*).

[i]Gunung Ile-Ile: AMNH 101308 (holotype of *Hyosciurus ileile*), 196507. Sungai Tolewonu: AMNH 226497–99. Sungai Sadaunta: AMNH 224618–20. Gunung Kanino: AMNH 225459–63.

[j]Gunung Kanino: AMNH 225483–87. Gunung Nokilalaki: AMNH 225464, 225466–79, 225481, 225482. Pegunungan Latimojong: AMNH 101309, 101310 (holotype of *Hyosciurus heinrichi*), 101311, 196506. Molengraff Range: BMNH 40.691b, 40.642, 40.643, 40.645–40.647.

travel routes (Overzichtskaart van het eiland Celebes, Schaal 1:1,250,000, "met aanduiding van de politieke indeeling, de organisatie van het bestuur, de bestaande en nog aan te leggen verkeerswegen en van de groote cultuur-en industrieele centra." Samengesteld op last van de N. I. Regeering. Published in 1909), and referred to in the text as "Raven's map." Coordinates for Musser's collection localities, as well as height above sea level for places for which elevations were not recorded by other collectors, were estimated from "JOINT OPERATIONS GRAPHIC-GROUND" topographic maps, scale 1:250,000, compiled by Mapping and Charting Establishment RE, 1969, and published

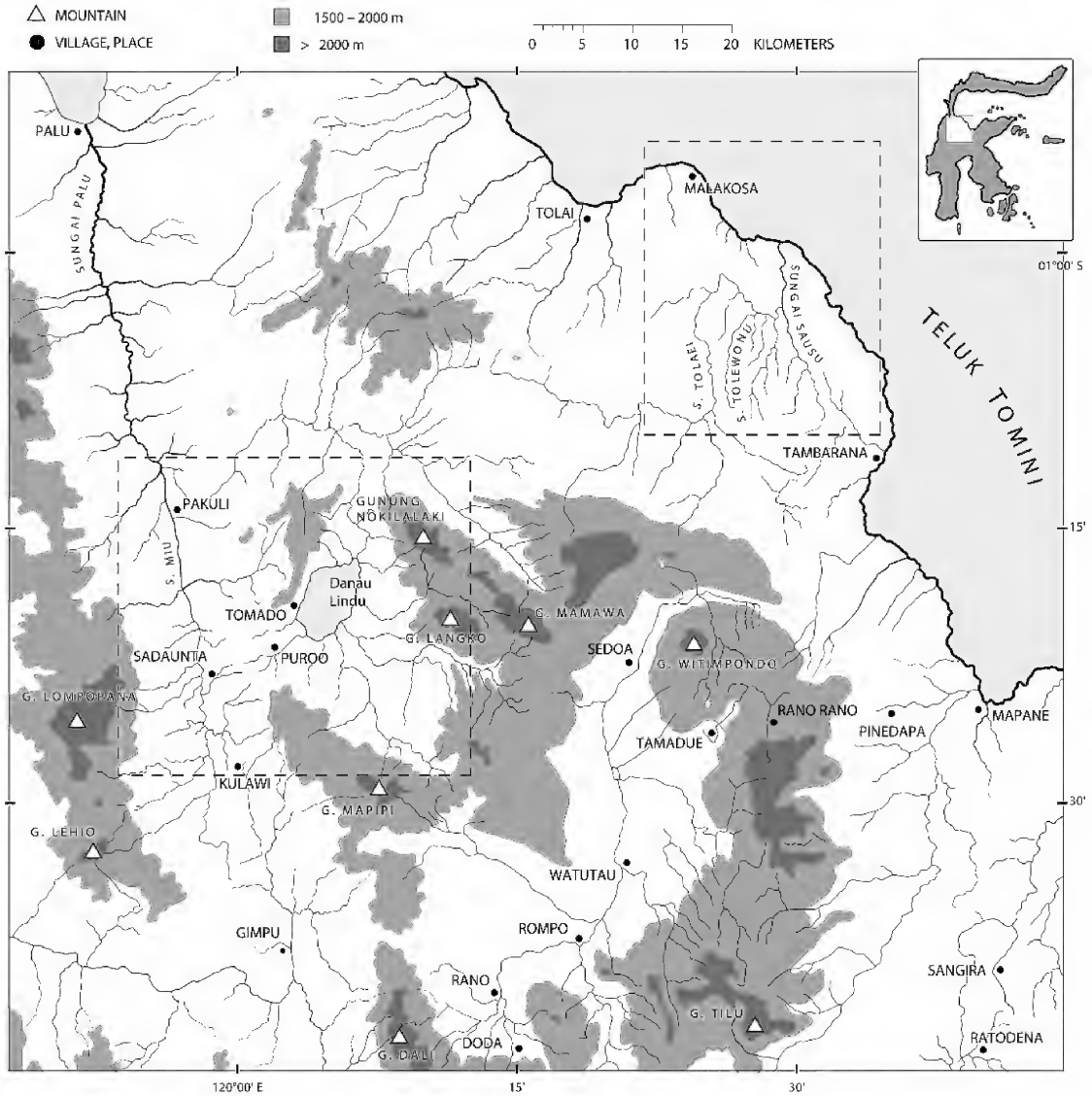

Fig. 3. The northern portion of Sulawesi's central core showing the two regions where Musser worked, the Danau Lindu (left dashed square) and Malakosa (right dashed square) areas. Three of H.C. Raven's sites where he collected squirrels are also on the map: Gunung Lehio, southwest of Kulawi; Pinedapa, west of Mapane; Rano Rano, in the mountains west of Pinedapa. Enlargement of the Danau Lindu area is shown in figure 4 on the opposite page. Figure 17 shows an enlargement of the Malakosa area.

by the Director of Military Survey, Ministry of Defence, United Kingdom, 1970, or by the Army Map Service, Washington, D.C. (Sheets NA 51-9 [1967], NA 51-12 [1967], NA 51-14 [1967], SA 50-8 [1971], SA 51-1 [1970], SA 51-5 [1967], and SA 51-14 [1967], SB 50-8 [1966], SB 51-1 [1970]). Gunung Topapu, the type locality for *Prosciurillus topapuensis*, was located by Thomas von Rintelen on an old map in the Berlin Museum that had been used by Paul and Fritz Sarasin, collectors of the holotype; a copy of the map was sent to Musser.

FORESTS: The tropical rain forests embracing the habitats of Sulawesi's endemic squirrel species will be described broadly by

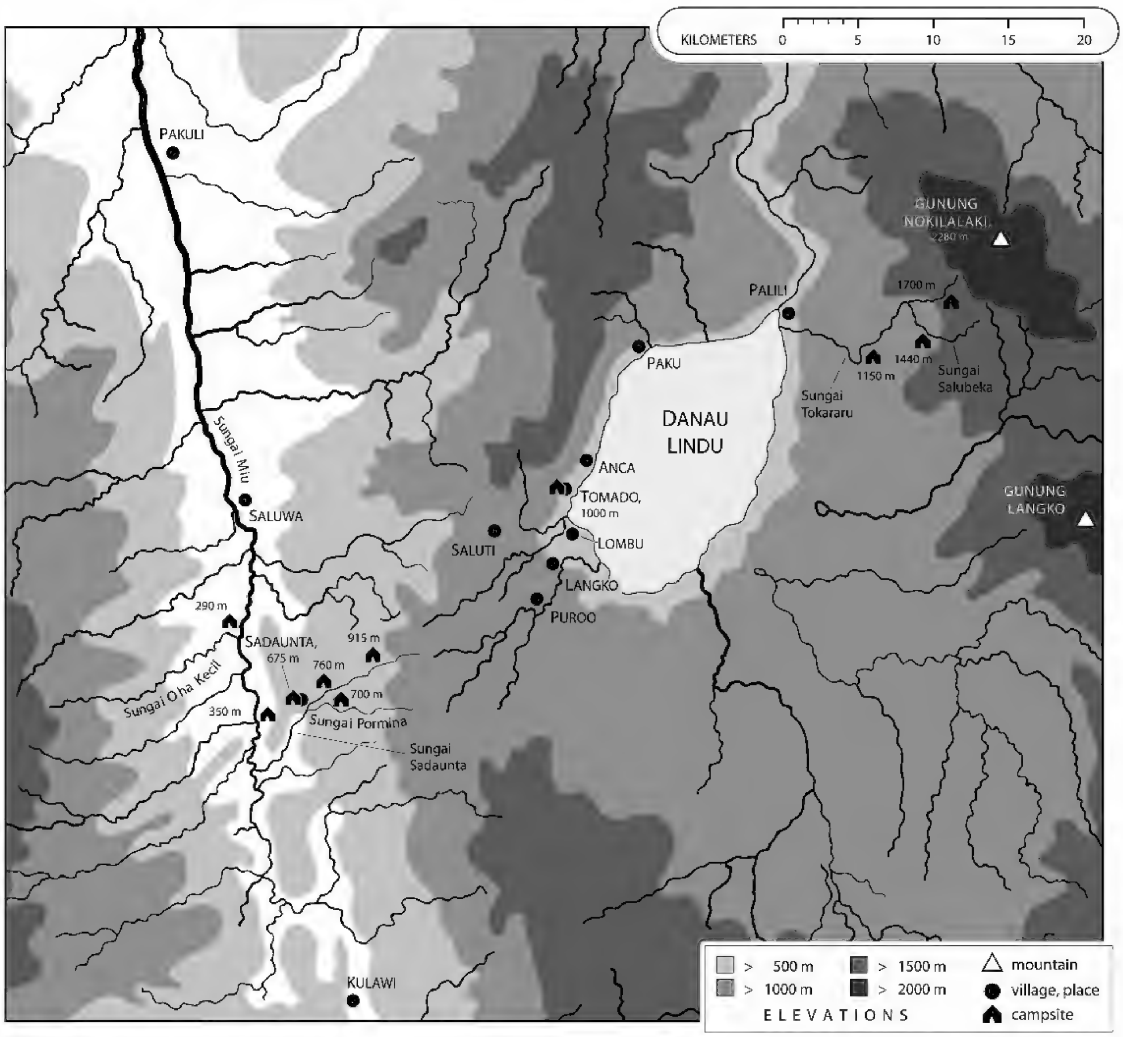

Fig. 4. The Danau Lindu area. Where the Sungai Oha Kecil flows into the Sungai Miu at 290 m was Musser's lowest camp along his transect; the summit of Gunung Nokilalaki was the highest place he worked. Tropical lowland evergreen rain forest embraces the area from the Sungai Oha Kecil to the camp along the Sungai Tokararu at 1150 m. The camp at 1440 m was on a ridge, Gunung Kanino, in lower montane rain forest. The lower camp at 1150 m was at the western end and base of the ridge. The highest camp at 1700 m was situated on the flanks of Gunung Nokilalaki, which at higher altitudes was covered with upper montane rain forest. *Prosciurillus topapuensis* and *P. murinus* occurred throughout the forests from the lower camps to Gunung Nokilalaki, *Rubrisciurus rubriventer* was encountered through much of the same altitudinal range but not higher than Gunung Kanino. Both species of *Hyosciurus* were trapped in the area, *H. ileile* in the lowlands and *H. heinrichi* on the mountain; the elevational ranges of each species abut at Gunung Kanino.

applying three of the forest formations categorized by Whitmore (1984): tropical lowland evergreen rain forest, tropical lower montane rain forest, and tropical upper montane rain forest. Whitmore's descriptions are very good and, as he notes, an extension and elaboration of P.W. Richards' (1952) classical "The Tropical Rain Forest," which readers will also find informative (a second edition was published in1996).

TABLE 2
Minimum and Maximum Ambient Air Temperatures Recorded from Coastal Lowlands to the Summit of Gunung Nokilalaki in Central Sulawesi[a]
Temperatures are summarized by mean and ranges (in parentheses). Abbreviations: G = Gunung, S = Sungai, K = Kuala.

		Temperature (°F)			
Elevation (m)	Place	Minimum	Maximum	Number of days	Period
2275	G. Nokilalaki	51.0 (48–54)	56.6 (52–63)	60	Mar. 4–May 2, 1975
2060	G. Nokilalaki	54.7 (51–58)	60.4 (54–65)	60	Mar. 4–May 2, 1975
1730	G. Nokilalaki	57.5 (55–66)	64.8 (61–69)	30	Dec. 6, 1973–Jan. 4, 1974
1440	G. Kanino	58.4 (52–61)	68.9 (63–76)	32	Jan. 16–Feb. 16, 1975
1150	S. Tokararu	61.1 (56–64)	73.9 (69–83)	32	Sept. 12–Oct. 13, 1973
758	S. Sadaunta	66.9 (62–70)	75.2 (70–86)	92	Sept. 16–Dec.16, 1974
290	S. Oha Kecil	70.1 (66–73)	78.8 (75–83)	37	July 31–Sept. 5, 1974
136	S. Tolewonu	69.8 (67–72)	77.3 (72–81)	57	Jan.3–Feb. 28, 1976
30	K. Navusu	73.6 (72–76)	80.9 (74–87)	95	Aug. 28–Nov. 30, 1975

[a]Each minimum and maximum recording was made during a 24-hour period. Thermometers were placed just above the ground beneath the canopy in primary forest. During each recording period, rain fell on most (about half to three-fourths) days. Relative humidities were about 100% in early mornings and late evenings and dropped to the low nineties and high eighties during the middle of each day. Data are from Musser's field journals.

The Sucking Lice

Institutions: Specimens examined and referred to in this report are deposited in the collections of the American Museum of Natural History, New York (**AMNH**); the Natural History Museum, London (**BMNH**); Lance A. Durden (**LAD**), the Museum Zoologicum Bogoriense, Cibinong, Java (**MZB**); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (**USNM**). Holotypes of all new species of lice described in this paper are deposited in the USNM.

Specimens, Procedures, and Abbreviations: Host squirrels were collected by W.J.C. Frost, I.A. Hanski, G. Heinrich, G.G. Musser, or H.C. Raven. Lice were removed from squirrel pelts by L.A. Durden. Description of the new species of lice presented in this paper follows the format and terminology of Kim (1966), Kim and Ludwig (1978), and Durden and Musser (1991, 1992). Drawings of entire lice conventionally illustrate dorsal structure to the left of the midline and ventral features to the right. Measurements were made using a calibrated micrometer inserted into the eyepiece of a high-power phase-contrast microscope. Only adult lice of the eight new species of Anoplura are described; a few immatures were collected for three of the new species but sample sizes were too small for reliable analyses. For two of the eight new species, only female lice were available; these two species were therefore excluded from the phylogenetic analysis.

Abbreviations for anatomical structures used in the descriptive portions of this work are as follows:

AnMHS	Anterior marginal head setae
ApHS	Apical head setae
DAcHS	Dorsal accessory head setae
DAnCHS	Dorsal anterior central head setae
DAnHS	Dorsal anterior head setae
DCAS	Dorsal central abdominal setae
DLAS	Dorsal lateral abdominal setae
DMHS	Dorsal marginal head setae
DMsS	Dorsal mesothoracic setae
DPaHS	Dorsal preantennal head setae
DPHS	Dorsal principal head setae
DPoCHS	Dorsal posterior central head setae
DPTS	Dorsal principal thoracic setae
OrS	Oral setae
PrS	Paratergal setae
SpAtHS	Supraantennal head setae

StAS	Sternal abdominal setae
SuHS	Sutural head setae
TeAS	Tergal abdominal setae
VCAS	Ventral central abdominal setae
VLAS	Ventral lateral abdominal setae
VPaHS	Ventral preantennal head setae
VPHS	Ventral principal head setae

PHYLOGENETIC ANALYSIS OF LICE: Phylogenetic analyses of 43 morphological characters for 14 taxa were performed using maximum parsimony (MP) and Bayesian approaches. PAUP*4.0b10 (Swofford, 2003) was used to perform equally weighted MP searches with 10,000 random addition replicates and tree bisection-reconnection (TBR) branch swapping. All characters were treated as unordered. To assess nodal support, nonparametric bootstrap analyses (Felsenstein, 1985) and computation of Bremer support indices (Bremer, 1988, 1994) were performed. Bootstrap analyses of equally weighted data were performed with 1000 pseudoreplicates and 10 random sequence additions per replicate using TBR branch swapping. Bremer support values were calculated using the program TreeRot v. 3 (Sorenson and Franzosa, 2007) using PAUP* (TBR branch swapping, 100 random addition sequences per calculation).

Bayesian phylogenetic analyses were performed using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Morphological characters were treated as standard and analyses were performed using the Mk model with a gamma distribution (Lewis, 2001). Bayesian analyses were initiated with random starting trees, run for 10 million generations with four incrementally heated chains (Metropolis-coupled Markov chain Monte Carlo; Huelsenbeck and Ronquist, 2001), and sampled at intervals of 1000 generations. To avoid entrapment on local optima, two independent Bayesian analyses were run and log-likelihood scores were compared for convergence (Huelsenbeck and Bollback, 2001; Leaché and Reeder, 2002). Log-likelihood scores of sample points were plotted against generation time to assess stationarity and all burn-in points (the first 2000 trees) were discarded. The retained equilibrium samples were used to generate a 50% majority rule consensus tree with the percentage of samples recovering any particular clade representing that clade's posterior probability.

Host and parasite trees were assessed for similarity using a tree-based method to consider similarities between trees as possible instances of codivergence. Tree-based methods compare only the branching structure of host and parasite trees to determine if more codivergence events are present than would be observed by chance. The host tree was compiled from the literature (Mercer and Roth, 2003). However, because of the polytomy among the three species of *Prosciurillus*, three different analyses were performed, each using a different combination of two of the three host species (*P. abstrusus* and *P. leucomus*, *P. abstrusus* and *P. murinus*, and *P. leucomus* and *P. murinus*) and their respective lice.

Reconciliation analysis (TreeMap 2.0β; Page, 1994; Charleston, 1998; Charleston and Page, 2002) was used to test for phylogenetic congruence between host and parasite trees. TreeMap 2.0β finds the least costly reconstruction of host-parasite relationships while maximizing the number of cospeciation events. The default settings of TreeMap were used (assigning a cost of zero for cospeciation events and a cost of 1 for host switches, losses, and duplications). The parasite tree was randomized 100 times and the observed number of cospeciation events was compared to the resulting null distribution of cospeciation events to determine whether the number of cospeciation events recovered from the reconciliation analysis was significant.

Our formal introduction to Sulawesi's endemic sciurid fauna begins with the following section reviewing the current classification of living squirrels.

ENDEMIC SULAWESI SQUIRRELS IN PHYLOGENETIC CONTEXT

We introduce the genera and species of endemic squirrels here by showing their phylogenetic position within the current classification of the Sciuridae as outlined by Thorington and Hoffmann (2005). The classification is also useful in understanding the placement of non-Sulawesi genera—both

New and Old World—from which sucking lice have been collected.

Efforts to convey evolutionary relationships within the Sciuridae by formal taxonomic classification extend back to the 19th century when Trouessart (1880) presented his classification. Ellerman (1940: 261) provided an instructive review of the various squirrel classifications published between 1891 and 1940. In the classification he adopted, the Sulawesi endemics were arranged in a broad "*Sciurus* Group" (as opposed to the "*Pteromys* Group" containing flying squirrels), which in turn was divided into seven "sections" or subgroups (Ellerman, 1940). The "*Sciurus* section" contained the Sulawesian species of tree squirrels that would later be placed in *Prosciurillus* and *Rubrisciurus* (Ellerman listed them in the *C. leucomus* and *C. rubriventer* groups within *Callosciurus*). The "*Lariscus* section" was another subgroup of genera that included the Sulawesian ground squirrels in *Hyosciurus*. Among the classifications reviewed by Ellerman was one constructed by Pocock (1923), which was based primarily on structure of the baculum, excluded flying squirrels, and is regarded by some researchers as the first modern classification of squirrels (Hoffmann et al., 1993; Thorington and Hoffmann, 2005), although Ellerman (1940: 262) noted that the review of sciurid dentition by Major (1893) formed the basis for most modern classifications of the Sciuridae.

Subsequent classifications published after 1940 ranged from the radical to the acceptable. Zahn (1942) proposed drastic changes in classification, all of which have been refuted by later researchers. In his seminal classification of mammals, Simpson (1945) recognized two groups, flying squirrels and all other squirrel genera, and built his classification of tree and ground squirrels primarily upon Pocock's (1923) framework; the Sulawesi tree squirrels remained in *Callosciurus*, which was arranged in the tribe Callosciurini, but surprisingly the ground squirrel genus *Hyosciurus* never made it into Simpson's classification.

By 1959, Moore proposed a classification of ground and tree squirrels derived from his study of cranial morphology, which incorporated Simpson's suprageneric groups and basically formed the framework of some subsequent classifications (Corbet and Hill, 1992; McKenna and Bell, 1997). Moore (1959) gathered together the Sulawesian tree squirrels, *Rubrisciurus* and *Prosciurillus*, and the ground squirrels, *Hyosciurus*, into the subtribe Hyosciurina of tribe Callosciurini, which also included the Bornean and Philippine pygmy tree squirrel *Exilisciurus*. In their compendium of mammals covering the Indomalayan Region, Corbet and Hill (1992) raised most of Moore's tribes to subfamily rank, and included the three Sulawesian genera in the Callosciurinae; McKenna and Bell (1997) placed the three genera in the tribe Nannosciurini, an older name for Callosciurini, and did not recognize the subtribe Hyosciurina, probably following Heaney (1985) who considered the subtribe to be undiagnosable.

Through the years various researchers have made or suggested small changes here and there in particular geographic groups and in targeted genera within whatever classification of Sciuridae prevailed at the time (see Howell [1938], Bryant [1945], Black [1963], Gromov et al. [1965], Hight et al. [1974], Hafner [1984], Thorington [1984], Heaney [1985], Corbet and Hill [1992], Thorington et al. [1996]; see also the reviews in Moore [1959], Hoffmann et al. [1993], and Thorington and Hoffmann [2005]). Some examples of relatively recent research results producing fresh insights into phylogenetic relationships within and among genera cover flying squirrels (Oshida et al., 2000a, 2000b; Oshida et al., 2001a; Thorington et al., 2002; Yu et al., 2004, 2006; Arbogast, 2007); Japanese species of Sciuridae (Oshida et al., 1996); species of *Sciurus* (Oshida and Masuda, 2000), *Callosciurus* (Oshida et al., 2001b), and *Dremomys* (Li et al., 2008); ground squirrels (Harrison et al., 2003; Herron et al., 2004; Helgen et al., 2009); marmots (Steppan et al., 1999); and chipmunks (Banbury and Spicer, 2007).

Up to 2005, all classifications or listings of genera in the Sciuridae, going back to Ellerman's 1940 arrangement, were initially divided into two groups at either the subfamily or family rank: flying squirrels as opposed to

ground and tree squirrels (Simpson, 1945; Mclaughlin, 1984; Corbet and Hill, 1992; Hoffmann et al., 1993; McKenna and Bell, 1997). Furthermore, all classifications that were implicitly accepted as recovered phylogenies were derived from anatomical features.

Beginning in the 1990s, analyses of gene sequences provided a new and incisive set of data that would be employed to recover the internal lineages of Sciuridae. Results from regional inquiries were combined with those from broader investigations to provide another estimate of evolutionary relationships among squirrel genera. Particularly influential were the results described in two publications: the phylogeny recovered by Mercer and Roth (2003), who analyzed nuclear IRBP, mitochondrial 12S, and 16S ribosomal DNA; and the relationships proposed by Steppan et al. (2004), who employed the nuclear genes c-myc and RAG1. Their results, among other phylogenetic insights, overturned the segregation of flying squirrels in a group separate from tree and ground squirrels (a pattern indicated also by Hight et al. [1974] using immunodiffusion technique, and by Herron et al. [2004] employing the mitochondrial cytochrome *b* gene to recover phylogenetic relationships of ground squirrels and other sciurids), highlighted the monophyly of the endemic Sulawesi genera, and forced "a revision of the higher level systematic arrangement of the Sciuridae ...," which Thorington and Hoffmann (2005: 754) adopted in their chapter covering Sciuridae for Mammal Species of the World (Wilson and Reeder, 2005). Below we repeat their classification, with the addition of the following five nomenclatural changes.

(1) We recognize Moore's (1959) Hyosciurina for *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* (but without *Exilisciurus*, which Moore had included). This subtribe highlights results of the analysis by Mercer and Roth (2003: 1570) indicating "that a single lineage of squirrels crossed Wallace's Line to give rise to the three genera ... and multiple species of squirrels on Sulawesi." We add to the classification the single species of *Rubrisciurus*, the seven species of *Prosciurillus*, and the two species of *Hyosciurus* that we recognize (see below; all in boldface). Listing the 10 species here introduces them in advance of the accounts that we provide in the section on taxonomy to follow.

(2) We accept Nannosciurinae (Major, 1895) as a senior synonym for Callosciurinae (Pocock, 1923), as McKenna and Bell did (1997: 125, forming a new rank, tribe Nannosciurini, instead of Simpson's Callosciurini). Thorington and Hoffmann (2005: 754) rejected Nannosciurinae, preferring to use Callosciurinae without explaining the reason behind this action. Their reluctance is mirrored in the earlier literature. Pocock's (1923) arrangement, thought by some to be the first modern classification of the Sciuridae, included *Nannosciurus* in his new subfamily Callosciurinae, apparently ignoring Major's earlier name. Simpson (1945: 79) also had a problem with Nannosciurinae, recognizing it as a prior name, but explaining that "the type genus of which [*Nannosciurus*] is now placed in the Callosciurini [a new rank coined by Simpson and derived from Pocock's Callosciurinae], but its retention is inadvisable because the concept that it is still used to designate is radically different and because *Nannosciurus* is in no way a type of the tribe as here considered, but on the contrary is considered of somewhat doubtful pertinence to it." Even Moore (1959) employed Callosciurini without any reference to Major's earlier name. To be valid, as expressed by Article 11.7.1 of the Code (ICZN, 1999: 12), a family-group name when first published before 1999 must "be a noun in the nominative plural formed from the stem of an available generic name [Art. 29] (indicated either by express reference to the generic name or by inference from its stem ...," which certainly describes the formation of Major's Nannosciurinae. And if the integrity of the Code is not to be compromised, the tenant of priority should be acknowledged: "The valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission" (Article 23.1, ICZN, 1999: 24). Within the context of the rules promulgated by the Code, Major's Nannosciurinae should replace Pocock's Callosciurinae, the action taken by McKenna and Bell (1997). *Nannosciurus* contains a species of pygmy tree

squirrel and represents but one of the morphologies present within the range describing tree squirrels, ground squirrels, and genera somewhat intermediate in anatomy between tree and ground squirrels that are contained in the monophyletic division springing from the molecular analysis of Mercer and Roth (2003). Is *Callosciurus*, the type genus of Callosciurinae Pocock (1923), any more morphologically typical or representative of such a diverse clade than is *Nannosciurus*, the type genus of the older Nannosciurinae Major (1895)?

(3) This modification to the classification by Thorington and Hoffmann (2005) is to place *Funambulus* and *Exilisciurus* in their own tribes to separate them from the rest of the genera in the larger Nannosciurine clade. Mercer and Roth (2003) identified the Indian *Funambulus* as an early monophyletic offshoot within the clade of Indomalayan tree and ground squirrels. (Immunological distances analyzed by Hight et al. [1974] also supported a strong link between *Funambulus* and Indomalayan squirrels.) Moore (1959: 170) had described several cranial traits peculiar to *Funambulus* (characters he used to define the subtribe Funambulina), which, combined with its unique molecular signature, justify tribal separation. The Bornean and Philippine *Exilisciurus* is another lineage recovered by Mercer and Roth (2003), one that separated from the nannosciurine ancestral stock later than *Funambulus* but earlier than the clade containing the remainder of the genera in Nannosciurinae (which are in Nannosciurini; see below); Steppan et al. (2004) also recovered *Exilisciurus* as basal to the Indomalayan genera sampled in their molecular analyses). Monogeneric tribes are unappealing to some taxonomists, but hierarchical nomenclatural designations highlight their distinctiveness in any linear arrangement of taxa within the sciurid classification. Characteristics of the new tribe are as follows.

Exilisciurini new tribe. Type genus: *Exilisciurus* Moore, 1958. Definition: arboreal, diurnal, small-bodied sciurids with tail shorter than head and body length (LT/LHB = 68%–78%); no facial or body stripes, no postauricular or nape patches, very long ear tufts in *E. whiteheadi*; plantar surface lacking hypothenar pad, and thenar reduced relative to interdigital pads; skull small, gracile, with marked cranial flexion; moderately long rostrum and globular braincase; long frontals and wide interorbit with notch in middle of dorsolateral margin of interorbit; postorbital processes small relative to size of skull, orbit short; maxillary tooth rows converge posteriorly; no partitions in ectotympanic bulla; blade of baculum with serrated edge (Pocock, 1923; Moore, 1959; Heaney, 1985; Payne et al., 1985).

(4) We list three genera of chipmunks instead of only one, following the assertions of Piaggio and Spicer (2000, 2001) and Banbury and Spicer (2007). The three monophyletic groups of New and Old World chipmunks those authors recovered from analyses of mitochondrial cytochrome *b* and cytochrome oxidase II genes, coupled with older published results from study of some anatomical systems referenced by them, convince us that *Tamias* applies to the chipmunk of the eastern United States, *Neotamias* to the many species indigenous to western North America, and *Eutamias* to the single Old World species.

(5) Finally, we add seven genera of ground squirrels that were formerly contained in *Spermophilus* as subgenera (Thorington and Hoffmann, 2005). These monophyletic clusters have been recently diagnosed using the combination of morphological traits, cranial and dental morphometrics, and clades recovered from phylogenetic analyses of mitochondrial cytochrome *b* (Harrison et al., 2003; Herron et al., 2004; Helgen et al., 2009).

Family Sciuridae Fischer de Waldheim, 1817
  Subfamily Ratufinae Moore, 1959
    Ratufa Gray, 1867
  Subfamily Sciurillinae Moore, 1959
    Sciurillus Thomas, 1914
  Subfamily Sciurinae Fischer de Waldheim, 1817
    Tribe Pteromyini Brandt, 1855
      Subtribe Pteromyina Brandt, 1855
        Aeretes G.M. Allen, 1940
        Trogopterus Heude, 1898
        Belomys Thomas, 1908
        Pteromyscus Thomas, 1908
        Aeromys Robinson and Kloss, 1915
        Biswamoyopterus Saha, 1981

Eupetaurus Thomas, 1888
Pteromys G. Cuvier, 1800
Petaurista Link, 1795
Subtribe Glaucomyina Thorington and Hoffmann, 2005
Eoglaucomys A.H. Howell, 1915
Glaucomys Thomas, 1908
Hylopetes Thomas, 1908
Petaurillus Thomas, 1908
Petinomys Thomas, 1908
Iomys Thomas, 1908
Tribe Sciurini Fischer de Waldheim, 1817
Tamiasciurus Trouessart, 1880
Sciurus Linnaeus, 1758
Rheithrosciurus Gray, 1867
Syntheosciurus Bangs, 1902
Microsciurus J.A. Allen, 1895
Subfamily Nannosciurinae Major, 1895
Tribe Funambulini Moore, 1959
Funambulus Lesson, 1835
Tribe Exilisciurini (new tribe; type genus is *Exilisciurus* Moore, 1958)
Exilisciurus Moore, 1958
Tribe Nannosciurini Major, 1895
Subtribe Hyosciurina Moore, 1959
Rubrisciurus Ellerman, 1954
Rubrisciurus rubriventer (Müller and Schlegel, 1844)
Prosciurillus Ellerman, 1947
Prosciurillus leucomus (Müller and Schlegel, 1844)
Prosciurillus alstoni (Anderson, 1879)
Prosciurillus weberi (Jentink, 1890)
Prosciurillus topapuensis (Roux, 1910)
Prosciurillus rosenbergii (Jentink, 1879)
Prosciurillus murinus (Müller and Schlegel, 1844)
Prosciurillus abstrusus Moore, 1958
Hyosciurus Archbold and Tate, 1935
Hyosciurus heinrichi Archbold and Tate, 1935
Hyosciurus ileile Tate and Archbold, 1936
Subtribe *Nannosciurina* Forsyth Major, 1895
Tamiops J.A. Allen, 1906
Dremomys Heude, 1898
Nannosciurus Trouessart, 1880
Sundasciurus Moore, 1958
Rhinosciurus Blyth, 1856
Menetes Thomas, 1908
Lariscus Thomas and Wroughton, 1909
Glyphotes Thomas, 1898
Callosciurus Gray, 1867
Subfamily Xerinae Osborn, 1910
Tribe Xerini Osborn, 1910
Atlantoxerus Major, 1893
Spermophilopsis Blasius, 1884
Xerus Hemprich and Ehrenberg, 1833
Tribe Protoxerini Moore, 1959
Myosciurus Thomas, 1909
Heliosciurus Trouessart, 1880
Protoxerus Major, 1893
Epixerus Thomas, 1909
Paraxerus Major, 1893
Funisciurus Trouessart, 1880
Tribe Marmotini Pocock, 1923
Sciurotamias Miller, 1901
Tamias Illiger, 1811
Eutamias Trouessart, 1880
Neotamias A.H. Howell, 1929
Ammospermophilus Merriam, 1892
Notocitellus A.H. Howell, 1938
Marmota Blumenbach, 1779
Otospermophilus Brandt, 1844
Callospermophilus Merriam, 1897
Spermophilus F. Cuvier, 1825
Ictidomys Allen, 1877
Poliocitellus A.H. Howell, 1938
Xerospermophilus Merriam, 1892
Urocitellus Obolenskij, 1927
Cynomys Rafinesque, 1817

Fifty years ago, the endemic squirrels on Sulawesi were shown to belong to a monophyletic cluster, a view derived from study of cranial anatomy (Moore, 1959). Forty-four years later that clade has been supported by results from molecular analysis (Mercer and Roth, 2003). We now work with the strong hypothesis that the three Sulawesian genera and their contained species likely evolved from a single lineage, an ancestor that crossed the Makassar Strait from the Sunda Shelf to Sulawesi sometime in the distant past between 11.4 to 10.5 million years ago (Mercer and Roth, 2003: 1571). Keeping in mind these relatively recent results from inquiries based on morphology and molecules, let us go back before Mercer and Roth, and before Moore, to read the insight expressed by Sir John R. Ellerman (1949: 14–15):

> If the Flying-squirrels are excepted, there are five main types of Squirrel plentifully distributed through the larger Malay Islands of Java, Borneo, and Sumatra, these being *Nannosciurus*

(pygmy squirrels with very short orbit), *Callosciurus* (normal tree-squirrels), *Ratufa* (giant tree-squirrels), *Lariscus* (simple-toothed striped squirrels), and *Rhinosciurus* (long-nosed squirrels). It is interesting that all of these *types* of Squirrel except *Lariscus* are represented in Celebes, however, by something quite distinct from the western islands; for instance, *Sciurilus murinus* ([= *Prosciurillus murinus*] Celebes pygmy squirrel with short orbit, but just a little too advanced and specialized to be congeneric with *Nannosciurus*); *Callosciurus leucomus* ([= *Prosciurillus leucomus*] typical tree-squirrel type from Celebes), but with the orbit more shortened than is normal in *Callosciurus* or Palaearctic *Sciurus*; *Callosciurus rubriventer* ([= *Rubrisciurus rubriventer*] Celebes giant squirrel) representing the giant *Ratufa* but with cranial characters of a large *Callosciurus*, and not those of *Ratufa*; and *Hyosciurus* (Celebes long-nosed squirrel) with completely different orbit length from its closest ally the Malaysian long-nosed genus *Rhinosciurus*.

This seems to suggest that there is, so to speak, a necessity for, or shall we say a "possibility of living" for each of these types of Squirrel in each of these islands. And it also suggests that if Celebes was early isolated from the other islands, it has produced each of these four types, closely paralleling those of the other islands, but from quite distinct ancestral types. Or perhaps, more briefly, that if one genus is absent in one island, then another will take its place there, developing an interesting superficial resemblance to the absent genus.

From Ellerman's penetrating exposition, we turn to the accounts that describe our view of the species forming Sulawesi's endemic tree and ground squirrel fauna.

THE ENDEMIC SULAWESI SQUIRRELS

Here we present accounts covering the one species of *Rubrisciurus*, the seven species of *Prosciurillus*, and the two species of *Hyosciurus*. We describe tree and ground squirrels exhibiting a wide range in body size (table 3) and inhabiting primary forest formations (table 4). Some species occur throughout Sulawesi in both evergreen lowland and montane rain forests, others are restricted to particular geographic regions and forest habitats, and one is an archipelago endemic (tables 4, 5). Geographic and altitudinal relationships among the species are reflected in their patterns of sympatry or parapatry (table 6).

Each genus is introduced with a brief review of its taxonomic history, an emended generic diagnosis, and introduction to its phylogenetic position within Sciuridae. Each species account includes information contained in the following 11 subheadings.

(1) A gazetteer of collection localities includes all specimens we examined from those places, the very few that we did not see but were dependably identified by our museum colleagues, and several based on reliable records from the published literature.

(2) Description of the type specimen and the locality from which the squirrel was collected. Some accounts contain formal designations of lectotypes and paralectotypes, and selection of a type locality. Several of the scientific names associated with species of *Prosciurillus* were proposed in the 1800s and early 1900s and based on more than one specimen, but the authors did not select a holotype, which was the usual convention at the time. Those early descriptions also did not always identify the institutions in which the voucher specimens supporting the descriptions were stored. Some samples were retained intact at a particular institution, others were divided and sent to different museums as examplars of the taxon described, and a few were sold and disappeared from any museum inventory. Fortunately, with the help of curators at different European and Asian museums (see acknowledgments), we located most of the material used in the early descriptions and can here identify appropriate specimens as holotypes or designate lectotypes and paralectotypes. Most type localities could be identified to town and geographic coordinates, a few were resolved only to a general region, and one had to be newly designated because the published indication of the locality was obviously incorrect.

(3) An emended species diagnosis.

(4) Descriptions of geographic and altitudinal distributions. The section also includes brief expositions of concordant distributions for other native mammal species.

(5) Description of the species, which focuses on physical body size and relative

TABLE 3
Contrasts in Body Size among Species of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*
Listed are ranges for lengths (mm) of head and body (LHB), tail (LT), hind foot (LHF), and ear (LE); LT/LHB (%); weight in grams (WT); lengths (mm) of skull (ONL) and maxillary tooth row (CLPMM). Data (from adults) are summarized from descriptive statistics presented in tables 7, 8, 15–17, 19, 26, 37, 38, and 43–45.
(The *P. leucomus* group is represented by *P. leucomus*, *P. alstoni*, and *P. topapuensis*—*P. weberi* and *P. rosenbergii* are excluded because of small sample size or incomplete sets of measurements.)

Species	LHB	LT	LT/LHB	LHF	LE	WT	ONL	CLPMM
Rubrisciurus								
R. rubrisciurus	250–305	180–255	82	67–77	25–33	500–860	64.6–71.6	11.1–14.0
Prosciurillus								
P. leucomus	165–188	140–190	95–98	43–47	—	—	44.1–47.6	7.1–8.0
P. alstoni	157–195	135–180	89–99	40–48	15–19	135–210	40.7–46.5	7.3–8.4
P. topapuensis	155–190	120–175	82–96	38–50	15–21	150–210	42.0–47.2	6.8–8.0
P. murinus	102–150	55–120	68–86	31–38	10–15	42–110	32.9–38.6	4.7–5.6
P. abstrusus	115–148	72–130	81	35–36	—	—	37.0–39.3	5.9–6.3
Hyosciurus								
H. heinrichi	195–240	65–120	45–47	51–61	21–26	228–370	59.9–67.3	9.5–11.2
H. ileile	213–250	70–125	48–49	53–60	21–22	293–520	56.7–63.1	9.2–10.1

sizes of appendages, color pattern of the fur, general conformation of the skull, and a few dental characters. We never intended to provide detailed descriptions of the skins, skulls, and dentitions as would be expected in a monographic treatment devoted to anatomy of the squirrels, but to concentrate on documenting those traits important in assessing fur color and patterning combined with qualitative and quantitative cranial and dental variation within and between species.

(6) Comparisons among the squirrels at the level of species. Intergeneric contrasts are highlighted in the emended generic diagnoses and addressed again in accounts of the type species of each genus. Within *Prosciurillus* and *Hyosciurus*, comparisons are made only among the species contained within each genus. Differences in coat coloration and patterning among the species of *Prosciurillus* are often pronounced, even spectacular, but cranial contrasts are quantitative in nature and often subtle, involving absolute size and proportions. Distinctions in coat color between the two species of *Hyosciurus*, however, are not pronounced but those centered on external and cranial dimensions, cranial proportions, and qualitative cranial traits are impressive.

(7) Geographic variation as analyzed by pelage color and pattern along with cranial and dental morphometrics. Noted here also is any biogeographic significance of the patterns revealed by the geographic variation.

(8) Ecology. The information includes observations of squirrels in the forest made by Durden on the northern peninsula and by Musser in the northern part of Sulawesi's central core. Habitat at trapping sites, diet, and reproductive activity are extracted from Musser's data gathered from his time working in primary forests.

(9) Ectoparasites. In addition to sucking lice, fleas, ticks, and mites are also part of the fauna parasitizing Sulawesi squirrels. While those parasite-host associations are not the focus of our report, we discuss the records and summarize their distributions on the host-species to provide a broader inventory of the ectoparasite fauna so far recorded from the tree and ground squirrels.

(10) A brief summary of sympatry with other squirrel species.

(11) A discussion of synonyms attached to a particular species.

Eight of the 10 squirrel species yielded samples of sucking lice, *Hoplopura* spp., all of which represent new species; each one is parasitic on a different species of squirrel. These eight species of lice are described in this report. Male and female lice were available for six of these samples (from

TABLE 4
Summary of Altitudinal Distributions (m) over the Mainland of Sulawesi for the Species of *Rubrisciurus*, *Hyosciurus*, and *Prosciurillus* Derived from Voucher Specimens

Species	Northern peninsula	Central core	East-central peninsula	Southeastern peninsula	Southwestern peninsula	Tropical rainforest formation
Rubrisciurus rubriventer	coast to 1067	30–1512	—	50–1400	300–600[a]	lowland evergreen to lower montane
Prosciurillus leucomus	coast to 1700	—	—	—	—	lowland evergreen to lower montane
Prosciurillus alstoni	—	31–1200	coastal plain	50–550	—	lowland evergreen
Prosciurillus weberi	—	coastal plain	—	—	—	lowland evergreen
Prosciurillus topapuensis	—	350–2800	—	—	—	lowland evergreen to upper montane
Prosciurillus sp.	—	—	—	—	0–100[b]	lowland evergreen
Prosciurillus murinus	coast to 1700	30–2200	—	50–500	1100–2000	lowland evergreen to upper montane
Prosciurillus abstrusus	—	—	—	1500–2000	—	lower to upper montane
Hyosciurus heinrichi	—	1479–2287[c] 1220–1312	—	—	—	lower to upper montane
Hyosciurus ileile	1700	168–1512	—	—	—	lowland evergreen to lower montane

[a]Known only by subfossil cranial fragments (see the account of *Rubrisciurus rubriventer*).

[b]Represented by a subfossil mandibular fragment from a specimen of the *Prosciurillus leucomus* group (*P. leucomus*, *P. alstoni*, *P. weberi*, *P. topapuensis*, and *P. rosenbergii*).

[c]The top range identifies collection sites in lower and upper montane forests that we regard as most reliable. Specimens listed in the gazetteer from Tamalanti lack elevation records, and those from Pegunungan Takolekaju (1220–1312 m), depending upon the local topography, could be at the lower limit of lower montane forest. On the western mountain block in the central core of Sulawesi, tropical evergreen rain-forest habitats usually dominate between 1006 and 1312 m. No reliable records place *H. heinrichi* outside of montane forest formations. At the base and lower slopes of Gunung Kanino between 1150 and 1400 m, Musser did not encounter *H. heinrichi* along this part of his transect. See discussion in the account of *H. heinrichi*.

Rubrisciurus rubriventer, *Prosciurillus topapuensis*, *P. murinus*, *P. abstrusus*, *Hyosciurus heinrichi*, and *H. ileile*). Lice in samples from two other species (*Prosciurillus leucomus* and *P. alstoni*) consist of females and nymphs whose anatomical traits provide less information for phylogenetic analysis but do indicate that they also sample two additional species, each unique to the squirrel host. Descriptions of the lice follow the sections covering taxonomy of the endemic and nonendemic squirrels.

Rubrisciurus Ellerman, 1954

The early aboriginal human inhabitants of Sulawesi's forests were likely very familiar with this large-bodied and beautiful red squirrel. However, *rubriventer*, the type-species of *Rubrisciurus*, did not come to the attention of European naturalists until the Dutch traveler E.A. Forsten obtained a specimen sometime during 1840 to 1842 and sent it to the museum in Leiden where it was studied, named, and described by Müller and Schlegel in 1844 as a species of *Sciurus*. The tree squirrels, *Prosciurillus leucomus* and *P. murinus*, were named and described (also as species of *Sciurus*) in the same publication; the three constitute the earliest formal taxonomic exposition of Sulawesi's endemic squirrel fauna. From the time Forsten's squirrel reached European awareness, *rubriventer* has been treated as an especially distinctive species endemic to Sulawesi. Eventually

TABLE 5
Summary of Island Distributions off the Mainland of Sulawesi and in Kepulauan Sangihe for Species of *Prosciurillus* Derived from Voucher Specimens[a]
See map in figure 28 for the archipelago distribution of *P. rosenbergii* and maps in figures 11 and 30 for insular distributions of *P. leucomus*, *P. alstoni*, and *P. murinus*.

Species	Off northeastern tip of northern peninsula	Off end of southeastern peninsula	Kepulauan Sangihe
Prosciurillus leucomus	Lembeh	—	—
Prosciurillus alstoni	—	Buton, Kabaena	—
Prosciurillus rosenbergii	—	—	Sangihe, Siao, Tahulandang, Ruang
Prosciurillus murinus	Talise, Lembeh	—	—

[a]No specific elevations are associated with any of the specimens. Highest points on Pulau Talise and Pulau Lembeh are 264 and 447 m, respectively, which would be in tropical lowland evergreen rain-forest formations.

Highest places for Pulau Buton and Pulau Kabaena are 1190 and 1570 m, respectively. On the mainland of the southeastern peninsula, *P. alstoni* occupies only lowlands, with no records of specimens above 550 m (see table 4).

Highest recordings for islands in Kepulauan Sangihe are: Pulau Sangihe, 1320 m, Pulau Siao, 1827 m, Pulau Tahulandang, 1320 m, and Pulau Ruang, 731 m. These islands consist of volcanos ringed by narrow bands of coastal lowlands. Squirrels could have been collected in tropical lowland evergreen rain forests on the coasts and/or higher on forested slopes of the volcanos.

transferred from *Sciurus* to *Callosciurus*, the morphology of *rubriventer* so impressed Ellerman (1940: 350) that he wrote "[the species] might perhaps form a distinct subgenus" and arranged it as the only member of a "*rubriventer* Group" in his annotated compilation of "The Families and Genera of Living Rodents."

Fourteen years later, Ellerman formalized his impression by appointing *rubriventer* as the type species for *Rubrisciurus*, which he considered to be a subgenus of *Callosciurus*. Large size was his primary diagnostic criterion. He first compared the species to Asian *Ratufa* and Bornean *Rheithrosciurus*, both containing species of large body size (see Medway, 1969; Payne et al., 1985), and eventually, but somewhat skeptically, to *Sciurus*, and finally was ambiguous about the relationship of *Rubrisciurus* to other squirrel genera:

> The generic position of *C. rubriventer* is not very clear as I do not think the structure of its baculum has been recorded, and *Callosciurus* essentially only differs from *Sciurus* in the structure of its baculum and its Indomalayan (instead of Palaearctic or American) habitat. But whatever the structure of the baculum in *C. rubriventer*, it stands so sharply apart from all other *Sciurus* and *Callosciurus* species of Europe and Asia that at least subgeneric rank seems required for it.

By 1959 Moore (1959: 176), using a combination of cranial traits, raised subgenus *Rubrisciurus* to generic level and placed it in the subtribe Hyosciurina, tribe Callosciurini along with the Sulawesian *Prosciurillus* and *Hyosciurus*, and the Sundaic-Philippine *Exilisciurus*. Corbet and Hill (1992: 305) recognized *Rubrisciurus* in their treatise on The Mammals of the Indomalayan Region but expressed a note of uncertainty: "This [*Rubrisciurus*] was described as a subgenus of *Callosciurus* mainly on the basis of its large size. Its relationship to *Callosciurus*, *Sundasciurus* and *Prosciurillus* is unclear." Earlier, Moore (1959) regarded *Sundasciurus* to be a member of the subtribe Callosciurina in the Callosciurini and did not consider it to be especially closely related to *Rubrisciurus*, which he placed in a different subtribe. Moore's hypothesis of phylogenetic relationships for *Rubrisciurus* has been vindicated in part by analyses of the nuclear IRBP and mitochondrial 12S and 16S ribosomal DNA used by Mercer and Roth (2003) to recover a squirrel phylogeny that included a monophyletic group containing *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* nested within a cladistic cluster formed by *Callosciurus*, *Sundasciurus*, and their relatives. Within the Sulawesian clade, *Rubrisciurus* is basal to *Prosciurillus* and *Hyosciurus*, and more closely related to the former than to the morphologically

TABLE 6
Summary of Distributional Sympatry over the Mainland of Sulawesi for the Species of *Rubrisciurus*, *Hyosciurus*, and *Prosciurillus* Derived from Voucher Specimens[a]

Species	Northern peninsula	Central core	East-central peninsula	Southeastern peninsula	Southwestern peninsula
Rubrisciurus rubriventer	*P. leucomus*, *P. murinus*	*P. topapuensis*, *P. alstoni*, *P. weberi*, *P. murinus*, *H. ileile*, *H. heinrichi*	—	*P. alstoni*, *P. murinus*	probably sympatric with *P.* sp. and *P. murinus* before forest removal
Prosciurillus topapuensis	—	*R. rubriventer*, *P. murinus*, *H. ileile*, *H. heinrichi*	—	—	—
Prosciurillus leucomus	*R. rubriventer*, *P. murinus*, *H. ileile*	—	—	—	—
Prosciurillus alstoni	—	*R. rubriventer*, *P. murinus*, *H. ileile*	only species recorded	*R. rubriventer*, *P. murinus*	—
Prosciurillus weberi	—	*R. rubrisciurus*	—	—	—
Prosciurillus sp.	—	—	—	—	probably sympatric with *R. rubriventer* and *P. murinus* before forest removal
Prosciurillus murinus	*R. rubrisciurus*, *P. leucomus*, *H. ileile*	*R. rubriventer*, *P. topapuensis*, *P. alstoni*, *H. ileile*, *H. heinrichi*	—	*R. rubriventer*, *P. alstoni*	only species recorded between 1100 and 2000 m; probably in lowlands with *R. rubrisciurus* and *P.* sp. before forest removal
Prosciurillus abstrusus	—	—	—	only species recorded between 1500 and 2000 m	—
Hyosciurus heinrichi	—	*R. rubriventer*, *P. topapuensis*, *P. murinus*, *H. ileile* (parapatric with *H. ileile*)	—	—	—
Hyosciurus ileile	*P. leucomus*, *P. murinus*	*R. rubriventer*, *P. topapuensis*, *P. alstoni*, *P. murinus*, *H. heinrichi* (parapatric with *H. heinrichi*)	—	—	—

[a] *Prosiurillus rosenbergii*, not listed in the table, is endemic to the islands constituting Kepulauan Sangihe north of the northeastern peninsula of mainland Sulawesi and is the only sciurid recorded from those islands (see table 5).

divergent ground squirrels in the latter. The phylogram of relationships generated by Mercer and Roth excludes the species of pygmy squirrels in *Exilisciurus* from the Sulawesian clade; it forms a monogeneric clade separate from both the Sulawesian clade and that containing *Callosciurus* and its allies, which includes *Nannosciurus*, the other group of Indomalayan pygmy squirrels. The pattern again supports Moore's (1958) hypothesis that the two genera of pygmy squirrels are not close phylogenetic allies, and acquired their specializations independently, but not the contention of Heaney (1985) who considered them to be closely related, or Corbet and Hill (1992) who regarded them as likely congeneric.

Because *Rubrisciurus* has never been adequately defined, we offer the following emended diagnosis. *Rubrisciurus* is distinguished from the other nannosciurine genera by the following combination of characters (see comparative measurements in table 3, compare skulls illustrated in figs. 6, 12–14, 36, and 37): **(1)** tree squirrel of large body size (table 3; among Indomalayan genera exceeded by only the Bornean *Rheithrosciurus* and Indomalayan *Ratufa*); **(2)** upperparts of head and back rich brown speckled with orange, buff, and black, surrounded by dark reddish fore legs and feet, shoulders, thighs, and hind legs and feet; **(3)** underparts bright reddish orange; **(4)** tail reddish brown and shorter than length of head and body, LT/LHB = 82%; **(5)** back of ears densely covered with glossy black hairs that project beyond pinnae margins to form prominent black tufts; **(6)** two pairs of inguinal teats; **(7)** cranium and mandible large and robust; **(8)** rostrum moderately long relative to rest of skull, nasals about as long as frontals and longer than width of interorbital region; **(9)** postorbital processes of frontals well in front of anterior surface of braincase ("well anterior to the posterior margin of the suborbit," Moore, 1959: 176); **(10)** prominent temporal ridges that converge to form a long sagittal crest one-third to three-fourths the length of the parietals, and anterior to the occiput; **(11)** anterior opening of the infraorbital canal lies slightly posterior to the premaxillary-maxillary suture and is concealed behind greatly projecting bony flange of the ventral root of the zygoma, the anteroventral corner of the flange considerably thickened and bearing a roughened outer surface for insertion of the superficial masseter; **(12)** jugal with high dorsal process, giving the zygomatic arch a robust conformation; **(13)** orbit short (indicated by lacrimal and posterior margin of zygomatic plate even with second upper molar); **(14)** posterior border of bony palate terminating anterior to backs of tooth rows, at middle of each third molar; **(15)** descending palatine vein typically transmitted through a notch (posterior maxillary notch) at the posterolateral margin of bony palate just caudad and slightly medial to end of tooth row (in about 10% of all skulls examined the opening is enclosed by bone forming a foramen); **(16)** pterygoid fossa long, narrow, and deep, its lateral margin formed by a high ridge (Moore's [1959] "ectopterygoid ridge"); **(17)** transbullar septa absent from most specimens, when present consists of half a septum, one septum, or one and one-half-septa (see Moore, 1959); **(18)** upper incisors strongly proodont (procumbent), emerging from the rostrum at an angle appreciably greater than 90°; **(19)** maxillary tooth rows parallel; **(20)** third upper premolar present, fourth premolar and three molars robust, all noticeably wider (lingual-labial length) than long (anterior-posterior distance). Among the other diagnostic traits Moore (1959: 176) listed were trenchant supraorbital notches and strongly convex lip of infraorbital canal; neither is characteristic of the skulls we examined.

Rubrisciurus shares fusion of temporal ridges anterior to the occiput with *Hyosciurus* (although the ridges fuse to form a very short sagittal crest in *Hyosciurus* compared with the much longer crest in *Rubrisciurus*). *Rubrisciurus* and *Prosciurillus* share presence of ear tufts (but not present in all species of *Prosciurillus*), posterior maxillary notch, flange concealing anterior opening of infraorbital canal and position of that opening relative to the premaxillary-maxillary suture, deep pterygoid fossa with prominent lateral pterygoid ridge, postion of posterior border of bony palate relative to end of tooth rows, proodont upper incisors, and wider than long fourth premolar and first two molars.

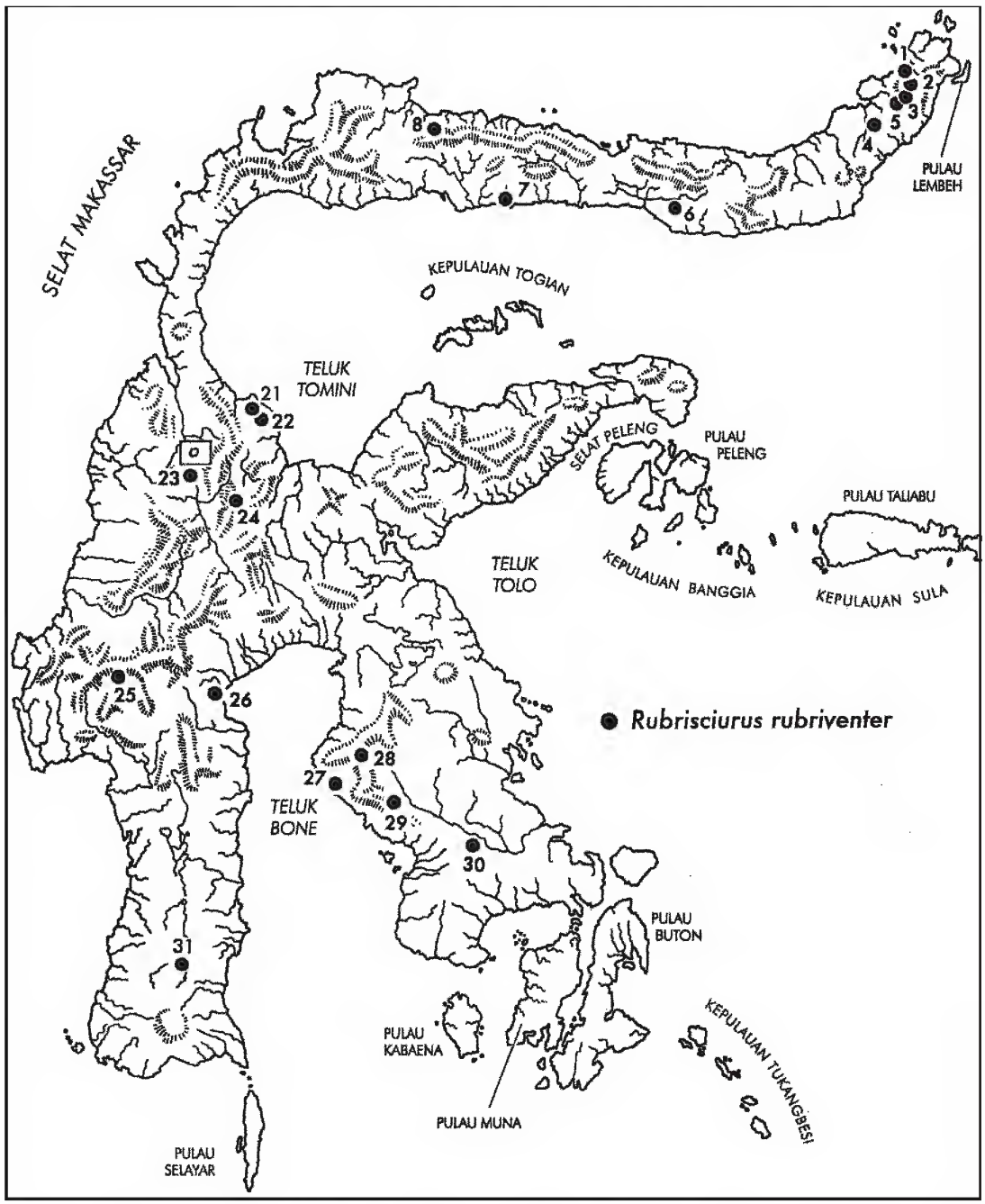

Fig. 5. Collection localities for samples of *Rubrisciurus rubriventer*. Numbers key to localities described in the gazetteer where specimens are also identified by museum initials and catalog numbers. The inset map, right (rectangle on larger map, above), contains collection sites (10–21) scattered along Musser's transect from the Sungai Oha Kecil to the slopes of Gunung Kanino. The dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and tropical lower montane forest.

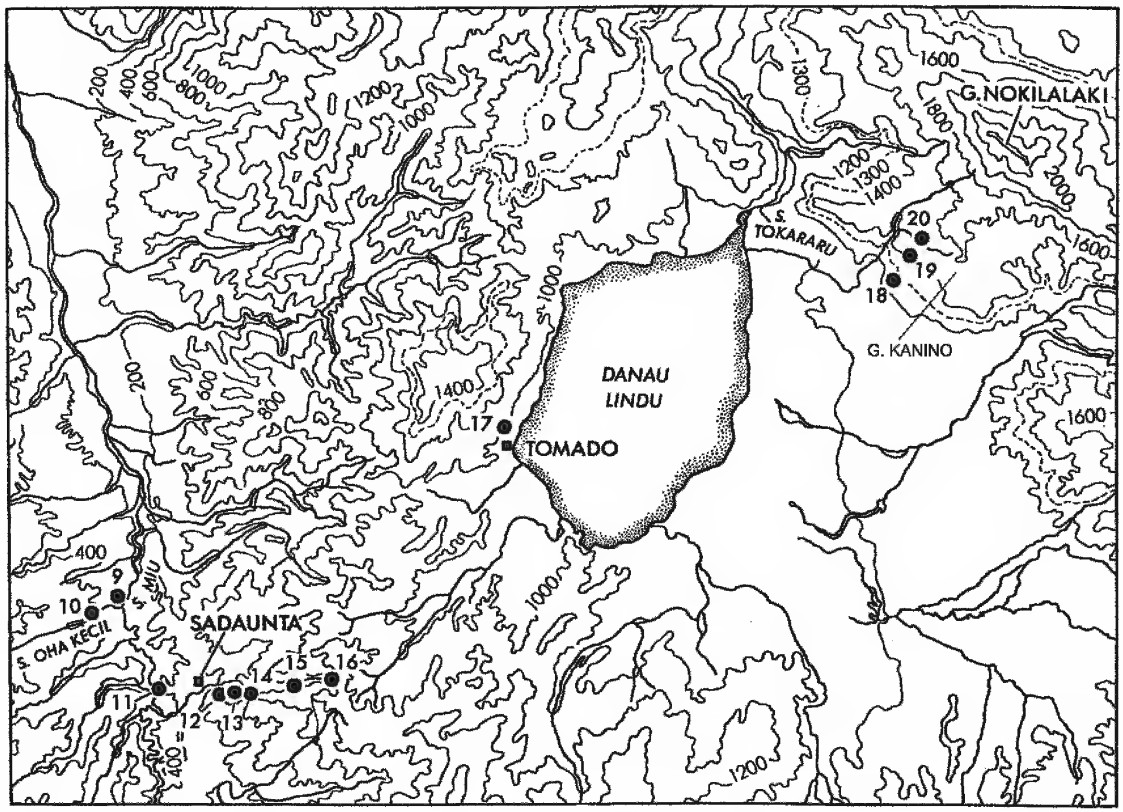

Fig. 5. *Continued.*

Our study of skins and skulls reaffirms the presence of a single species in *Rubrisciurus*, the definition of which we document below, along with its geographic and altitudinal distributions on Sulawesi derived from the collection localities of voucher specimens. *Rubrisciurus rubriventer* also hosts a morphologically very distinctive species of sucking louse (see the descriptions of the new species of *Hoplopleura* below).

GAZETTEER AND SPECIMENS EXAMINED: Collection localities for the 92 specimens of *R. rubriventer* studied are listed below. The number preceding each locality keys to a symbol on the map in figure 5.

1. **Manado** (also spelled "Menado"), 01°30′N, 124°50′E, coastal plain near sea level: RMNH specimens "*d–g*" in Jentink's (1888: 23) catalog; ZMA 15.933, 19.832, 19.833.
2. **Rurukan**, 01°21′N, 124°52′E: AMNH 196509 (500 m), 101324 (1000 m).
3. **Gunung Masarang**, 01°19′N, 124°51′E, 3500 ft (1067 m): BMNH 97.1.2.14.
4. **Temboan**, on Kuala Kalait, "a new clearing of eight houses and lies from Mt. Sapoetan south, 55° west and about six miles from Loboe," wrote Raven in his field journal, 1916: 3 (in Mammal Division Library at USNM), 01°03′N, 124°33′E (estimated from Raven's map), 500 m (estimated from Sheet NA 51-12): USNM 217824, 217905.
5. **Tomohon**, 01°19′N, 124°49′E, 700–800 m (estimated from Sheet NA 51-12): BMNH 99.10.1.7; NMB 3329, 1201/9538. Meyer (1899: 22) reported specimens from here.
6. **Tulabolo** ("Toelabello" in Jentink's catalog, 1888: 23), 00°31′N, 123°16′E, 760 ft (230 m; see Fooden, 1969: 137, for details): RMNH: specimen "*c*" in Jentink's (1888: 23) catalog. "**Modélido**," someplace in the Tulabolo-Gorontalo area east of Bumbulan: RMNH: specimen "*b*" in Jentink's (1888: 23) catalog.
7. **Bumbulan**, 00°29′N, 122°04′E, coastal plain near sea level: AMNH 153909–11, 153279; MZB 6257.
8. **Gunung Ile-Ile**, 00°58′N, 121°48′E, 500 m: AMNH 101321–23, 196508.

9. Valley of Sungai Miu, **Sungai Oha Kecil** (small tributary on left side of Sungai Miu), 01°22′S, 119°57′E (near confluence with Sungai Miu; estimated from Sheet SA 50-8), 290 m: AMNH 224621, 224622.
10. **Sungai Oha Kecil**, 1300 ft (396 m): AMNH 224623.
11. Valley of Sungai Miu, **Sungai Miu** (right side), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 350 m: AMNH 224055, 224056.
12. Valley of Sungai Miu, **Sungai Sadaunta** (also spelled "Sidaonta" or "Sidaunta"; tributary on right side of Sungai Miu), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 675 m: AMNH 224052–054.
13. **Sungai Sadaunta**: 2500 ft (762 m), AMNH 224624; 2550 ft (777 m), AMNH 224629; 2600 ft (793 m), AMNH 224625.
14. **Sungai Sadaunta**: 2700 ft (823 m), AMNH 224626.
15. **Sungai Sadaunta**: 3050 ft (930 m), AMNH 224628, 226839, 226840.
16. **Sungai Sadaunta**, 3300 ft (1006 m): AMNH 224627.
17. Valley of Danau Lindu, **Tomado** (a village on western shore of Danau Lindu), 01°19′S, 120°03′E (estimated from Sheet SA 5-8), 1000 m: AMNH 223023–025, 223466, 223467, 224057; USNM 218711.
18. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 4180 ft (1274 m): AMNH 223552.
19. **Gunung Kanino**, 4600 ft (1402 m), AMNH 225488; 4650 ft (1418 m), AMNH 225489, 225490.
20. **Gunung Kanino**, 4960 ft (1512 m): AMNH 225491.
21. Malakosa, **Kuala Navusu**, 00°58′S, 120°27′E (estimated from Sheet SA 51-1): 100 ft (30 m), AMNH 226052–054; 130 ft (40 m), AMNH 226055, 226056; 150 ft (46 m), AMNH 226058; 200 ft (61 m), AMNH 226057; 400 ft (122 m), AMNH 226059; 500 ft (152 m), AMNH 226060, 226061; 800 ft (244 m), AMNH 226062.
22. Tolai, **Sungai Tolewonu**, 01°04′S, 120°27′E (estimated from Sheet SA 50- 8): 500 ft (152 m), AMNH 226526, 226528–31; 540 (165 m), AMNH 226527; 550 ft (168 m), AMNH 226532; 750 ft (229 m), AMNH 226533; 850 ft (259 m), AMNH 226534; 1000 ft (305 m), AMNH 226535.
23. **Kulawi**, 01°27′S, 119°59′E, 500 m: USNM 218710.
24. **Besoa**, 01°44′S, 120°13′E (for "Besoa District," HOUSND, 1944): USNM 219522. H.C. Raven, who collected the squirrel in 1917, noted that "Besoa is a large level plain, undoubtedly a former lake bed, surrounded by mountains, which are covered by heavy forests; the tops of most of the mountains are above 2000 meters, the level plain is said to be about 1300 meters, or perhaps more. The plain is perhaps 2 or 3 miles wide by about 3 miles long and most of the area is covered with several varieties of long coarse grasses and reeds; in several places there are wet rice fields and the natives have made a few clearings on the lower slopes of the mountains. In some places the lower slopes are covered with grass" (Riley, 1924: 3). Raven collected animals from at least two places in the Besoa region (Doda and Gunung Taewo). No elevation or precise provenance is associated with USNM 219522.
25. Pegunungan Quarles, **Bulu (Gunung) Karua** (referred to as "Rantekaroa, Quarles Mt." on specimen tags), 02°56′S, 119°39′E, 4000 ft (1220 m): BMNH 40.674.
26. **Palopo**, 03°00′S, 120°12′E, coastal plain near sea level: MZB 6258–60.
27. **Wawo**, on the plain between the coast and western foothills of Pegunungan Mekongga (also spelled "Mengkoka"), 03°41′S, 121°02′E, 50 m: AMNH 101314–16.
28. Pegunungan Mekongga (also spelled "Mengkoka"), **Tanke Salokko** (the highest spot in Pegunungan Mekongga; see the maps and discussion in Heinrich [1932] and Stresemann [1940]), 03°35′S, 121°15′E (for the Pegunungan): 600 m, AMNH 101313; 1400 m, AMNH 101312.
29. Pegunungan Mekongga, **Masembo**, which is southeast of Wawo and the highest place in the southern portion of Pegunungan Mekongga (see maps and discussion in Heinrich [1932] and Stresemann [1940]), 03°35′S, 121°15′E (for the Pegunungan), 550 m: AMNH 101317–19.
30. **Lalolei** (spelled "Lalolis" on specimen tags and some maps), 03°57′S, 122°03′E, 300 m: AMNH 101320.
31. **Lamoncong** ("Lamontjong" is the older spelling), in the upper part of the Walanae River Valley, approximately 05°S, 119°50′E (see map in Mulvaney and Soejono, 1970: 164, and Bulbeck, 1996: 1014), 300–600 m: subfossil fragment of a skull described by Sarasin (1905: 47) from a limestone cave. We have not seen this specimen, but Sarasin described what can only be an example of *Rubrisciurus*, and he identified it as "*Sciurus rubriventer* Müll. Schl.?"

The following specimens were studied but the places where they were caught have not been mapped.

A. **"Célèbes"** (see Jentink, 1888): RMNH 13341 (specimen "*a*" in Jentink's [1888: 23] catalog; holotype of *Sciurus rubriventer*); see account of type locality. **"Celebes"**: BMNH 40.675, 43.238.

B. Central Core, **Tamalanti:** BMNH 40.691a. Laurie and Hill (1954: 156) noted that Tamalanti is a "Plantation between Rantekaroa [02°50′S, 119°50′E] and Koelawi [01°27′S, 119°59′E]," which was also the only information Musser and Paula Jenkins found when they searched through fieldnotes and other documents at BMNH. No elevation is provided for the specimen, but most collections from Tamalanti came from 3300–3800 ft (1006–1159 m) according to Paula Jenkins (personal commun.).

C. **"Tannya"**: FMNH 8328. We could not locate this place.

Rubrisciurus rubriventer
(Müller and Schlegel, 1844)

Sciurus rubriventer Müller and Schlegel, 1844: 86.

HOLOTYPE AND TYPE LOCALITY: The holotype of *Rubrisciurus rubriventer* is an adult male (RMNH 13341, specimen "*a*" in Jentink's [1888: 23] catalog) obtained by E.A. Forsten sometime during 1840–1842. It consists of a skin mounted in a live position; no skull is present. The skin apparently was in bad condition when prepared; most fur on the abdomen, right flank, caudal part of the left flank, and part of the left thigh is missing.

The type locality is "Célèbes," as listed in Jentink's (1888: 23) catalog. Forsten obtained most of his material in the region near the tip of the northeastern peninsula, which is in the administrative district of Minahasa (Kabupaten Minahasa), between 1° and 2° north latitude, Propinsi Sulawesi Utara, Indonesia. Laurie and Hill (1954: 94) indicated "Minahasa, north Celebes" to be the type locality, which restricted the location to that political unit. However, the type locality should rather be defined as "NE Celebes" (= NE Sulawesi) because Forsten also worked in the area of Gorontalo and as far west as Paguat (September–November 1841; see Van Steenis-Kruseman [1950: 179] and Forsten's unpublished diary in the archives of the Leiden Museum); hence, it cannot be excluded that specimens from that area are among Forsten's material (C. Smeenk, in litt., 2008). For additional information covering Forsten's travels in northeastern Sulawesi, see the account of *Prosciurillus leucomus*.

EMENDED DIAGNOSIS: *Rubrisciurus* is monotypic so the emended generic diagnosis applies to the species, *R. rubriventer*.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: Voucher specimens reflect a distribution throughout most of the mainland of Sulawesi; no material has been collected from offshore islands (see gazetteer and map in figure 5). Most collection records are in regions that are or were covered with primary tropical lowland evergreen rain forest. A few samples come from mountains at altitudes where tropical lower montane rain forest dominates (Gunung Kanino in the central core, and Pegunungan Mekongga on the southeast peninsula). No specimens have been collected from high elevations in cool and wet upper montane rain forest.

Provenances for modern specimens cover most of Sulawesi; only the east-central peninsular extension of the central core, which has not been surveyed for small mammals in any adequate endeavor, and the southwestern peninsula lack modern records. Unfortunately, except for some forested limestone tracts and higher slopes of the volcano Gunung Lompobatang, the southwestern peninsula has mostly been deforested; the former forest cover has been converted to farms and tree plantations from about 1700 m to the coastal lowlands (Fraser and Henson, 1996; see the map showing remaining forest tracts in Froehlich and Supriatna, 1996; and map 8d in MacKinnon, 1997). But, *Rubrisciurus* did occur there in prehistoric times as documented by a subfossil cranial fragment excavated from a rockshelter at Lamoncong, in the southern part of the peninsula northeast of Ujung Pandang (Sarasin, 1905). Archaeological artifacts from Sulawesi rockshelters are usually associated with the period of Toalean prehistory, 7000–5500 years B.P. (see references in Bulbeck, 1996). There are numerous prehistoric cave sites in the southern peninsula (Bulbeck, 1996) but, with the exception of the Lamoncong site, remains of *Rubrisciurus* have not been identified in the large samples of subfossil material excavated from some of them (as determined by Musser's study of subfossil cranial and dental remains).

In most other surveyed geographic regions of Sulawesi, *Rubrisciurus rubriventer* occurs with a member of the *Prosciurillus leucomus* group, with *P. murinus*, and with the two species of ground squirrels, *Hyosciurus ileile* and *H. heinrichi* (table 6). *Hyosciurus* has not been recorded from the southwestern peninsula. A member of the *P. leucomus* group is represented by a subfossil fragment from a cave deposit in the region (see account of *Prosciurillus* sp.). Modern samples of *P. murinus* have been collected from the southwestern peninsula but only above 1100 m on foothills and higher slopes of Gunung Lompobatang (see gazetteer), which is still clothed by some forest: the upper forested slopes of the volcano form an island "in a sea of densely-populated agricultural land east of Ujung Pandang" (Whitten et al., 1987: 519). So all three species of tree squirrels are now represented by subfossil or modern specimens from the southwestern arm. Murid rodents (rats) occurring with *Rubrisciurus* in lowland and lower montane forest formations in other geographic regions of Sulawesi (*Taeromys celebensis*, *Taeromys punicans*, *Bunomys chrysocomus*, *Bunomys andrewsi*, *Rattus hoffmanni*, and *Paruromys dominator* are examples) either live on the southwestern peninsula now or did in the past (Musser, 1984).

Elevational distributions gleaned from collection data tied to voucher specimens (see gazetteer) for three regions of Sulawesi are summarized here. On the northern peninsula, records extend from the coastal plain to 1067 m on Gunung Masarang. All places are within the elevational distribution of tropical lowland evergreen rainforest habitats. Specimens obtained in the central core of the island bracket habitats from the coastal plain at 30 m (Kuala Navusu) to those in the mountains (Gunung Kanino at 1512 m), and range from tropical lowland evergreen rain forest to tropical lower montane rain forest; Musser did not trap or see *R. rubriventer* in the forests above approximately 1500 m. Lower montane forest at 1400 m on Tanke Salokko in Pengunungan Mekongga is the highest collection record for *R. rubriventer* on the southeastern peninsula of Sulawesi; all other records lie within 50 to 500 m in tropical lowland evergreen rainforest environments.

DESCRIPTION: The original description of *rubriventer* (as a species of *Sciurus*) by Müller and Schlegel (1844: 86) is short (translated from the original in Dutch by Chris Smeenk [in litt., 2008]; the Dutch text is reproduced in appendix 2):

> 5.) **Sciurus rubriventer**, Forsten, n. sp. Size, shape and colour, generally as in the preceding species [*Sciurus hippurus*, now *Sundasciurus hippurus*, a large-bodied reddish species native to Malaya, Sumatra and Borneo; see Corbet and Hill, 1992, and Payne et al., 1985]; but the ears larger and much more strongly covered with black hairs, which are very long, hence protrude far above the ears. The brownish-red of the lower parts extends not only over the inner, but also over the outer sides of the legs. Hairs of the tail black, toward the tips with broad, faintly reddish-brown rings. Celebes.

Rubrisciurus rubriventer is the largest-bodied of the species of tree squirrels endemic to Sulawesi (length of head and body, 250–305 mm; length of hind foot, 67–77 mm; weight, 500–860 g; see tables 2, 7) and one of the largest of the tree squirrels and ground squirrels that are native to the Indomalayan region. It is exceeded in body size only by species of *Ratufa* (weight = 875–1620 g for Malayan and Bornean *R. bicolor* and *R. affinis*; see Medway, 1969: 56, and Payne et al., 1985: 233) and the Bornean endemic, *Rheithrosciurus macrotis* (weight = 1170–1280 g; see Payne et al., 1985: 243).

The color pattern, resplendent in its richly pigmented red and orange hues, of the large-bodied and long-legged *R. rubrisciurus* is best described this way: a reddish brown tail; reddish underparts, forelegs and feet, shoulders, thighs, hind legs and feet; brownish head and back speckled by buff, orange and black; ears highlighted by prominent glossy black tufts. The short fur (6–8 mm thick) covering the entire underparts, from chin to base of tail, is a rich, bright, reddish orange, which darkens to reddish maroon over dorsal surfaces of the front legs and feet, shoulders, along sides of the body and thighs, and dorsal surfaces of hind legs and feet. The top and sides of the head, and rest of the dorsum from the head to base of the tail, are covered by a thick (15–20 mm), rich brown coat flecked with buff, orange, and black (a

TABLE 7

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g), Derived from Samples of *Rubrisciurus rubriventer*[a]

Mean ± 1 SD, observed range (in parentheses) and size of sample are listed. Mean values were used to compute LT/LHB. Specimens measured are listed below.[b]

Variable	Northeastern peninsula (Temboan)	Central core (Sungai Oha Kecil, Sungai Miu, Sungai Sadaunta, Tomado)	Central core (Gunung Kanino)	Central core (Kuala Navusu, Sungai Tolewonu)	Central core (all samples combined)
LHB	280	282.9 ± 9.83 (265–305) 19	278.0 ± 4.47 (270–280) 5	280.6 ± 13.17 (250–305) 20	281.3 ± 11.03 (250–305) 44
LT	255	231.1 ± 14.10 (180–245) 19	229.0 ± 16.73 (200–240) 5	230.6 ± 15.00 (190–255) 18	230.6 ± 14.43 (180–255) 42
LT/LHB (%)	91	82	82	82	82
LHF	67	72.6 ± 2.52 (67–77) 19	71.8 ± 1.64 (70–73) 5	71.5 ± 1.50 (68–74) 20	72.0 ± 2.06 (67–77) 44
LE	—	30.0 ± 1.80 (26–33) 19	28.4 ± 2.70 (26–33)	28.2 ± 1.60 (25–31) 20	29.0 ± 1.99 (25–33) 44
WT	—	730.3 ± 65.18 (570–860) 17	698.0 ± 94.71 (530–750) 5	736.8 ± 75.56 (500–820) 20	729.5 ± 72.98 (500–860) 42

[a]Values for the squirrel from Temboan were obtained by the collector, H.C. Raven, who did not measure ear length or determine weight. All the specimens constituting the samples from central Sulawesi were measured by Musser in the field.

[b]Temboan: USNM 217824. Sungai Oha Kecil: AMNH 224621–23. Sungai Miu: AMNH 224055, 224056. Sungai Sadaunta: AMNH 224052–54, 224624–29, 226839, 226840. Tomado: AMNH 223023–25, 223467, 224057. Gunung Kanino: AMNH 223552, 225488–91. Kuala Navusu: AMNH 226052–57, 226059–62. Sungai Tolewonu: AMNH 226526–35.

combination provided by the overhairs with dark gray bases, subterminal buff or orange bands, and black tips, along with black guard hairs). There is a dark crescent above each eye, and the eye is circled by a wide buffy ring. The ears conspicuously contrast with the head, neck, back, and rump because the medial surface of each pinna is covered by soft black hairs that converge to form a tuft 5–10 mm long projecting beyond the contour of the dorsal pinna margin, and rimming the posterior margin (top and back edges of the pinna are defined by the black hairs, but the long tuft is confined to the dorsal margin). Color and extent of this tufting is closely similar to that present in *P. leucomus*. The tail of *R. rubriventer* is shorter than length of the head and body (LT/LHB = 82%), both dorsal and ventral surfaces are dark reddish brown (approaching maroon in some individuals), without the darker or paler borders formed by distal banding patterns of the hairs that are common to species of *Prosciurillus*.

The juvenile coat exhibits a color pattern similar to that of adults but the fur is thinner (hairs are finer), shorter, and the coloration typically duller, the red tones muted instead of being rich and bright.

Females have four teats arranged in two inguinal pairs. A single embryo was found in each of the few females of *Rubrisciurus rubriventer* caught by Musser.

Views of the large, stocky skull of *R. rubriventer* are illustrated in figure 6. Note the robust and relatively long rostrum, prominent anterior projection of the zygomatic root concealing the anterior opening of the infraorbital canal, high dorsal process of the jugal component of the zygoma, short orbit, position of the postorbital process well in front of the anterior margin of the braincase, prominent temporal ridges that unite to form a strong sagittal crest, posterior margin of the bony palate situated anterior to the backs of the parallel tooth rows, proodont (procumbent) upper incisors, wide fourth premolar and molars, and sturdy dentary with its high ramus.

Another trait bears inspection. At each posterolateral margin of the bony palate just caudal and slightly medial to the end

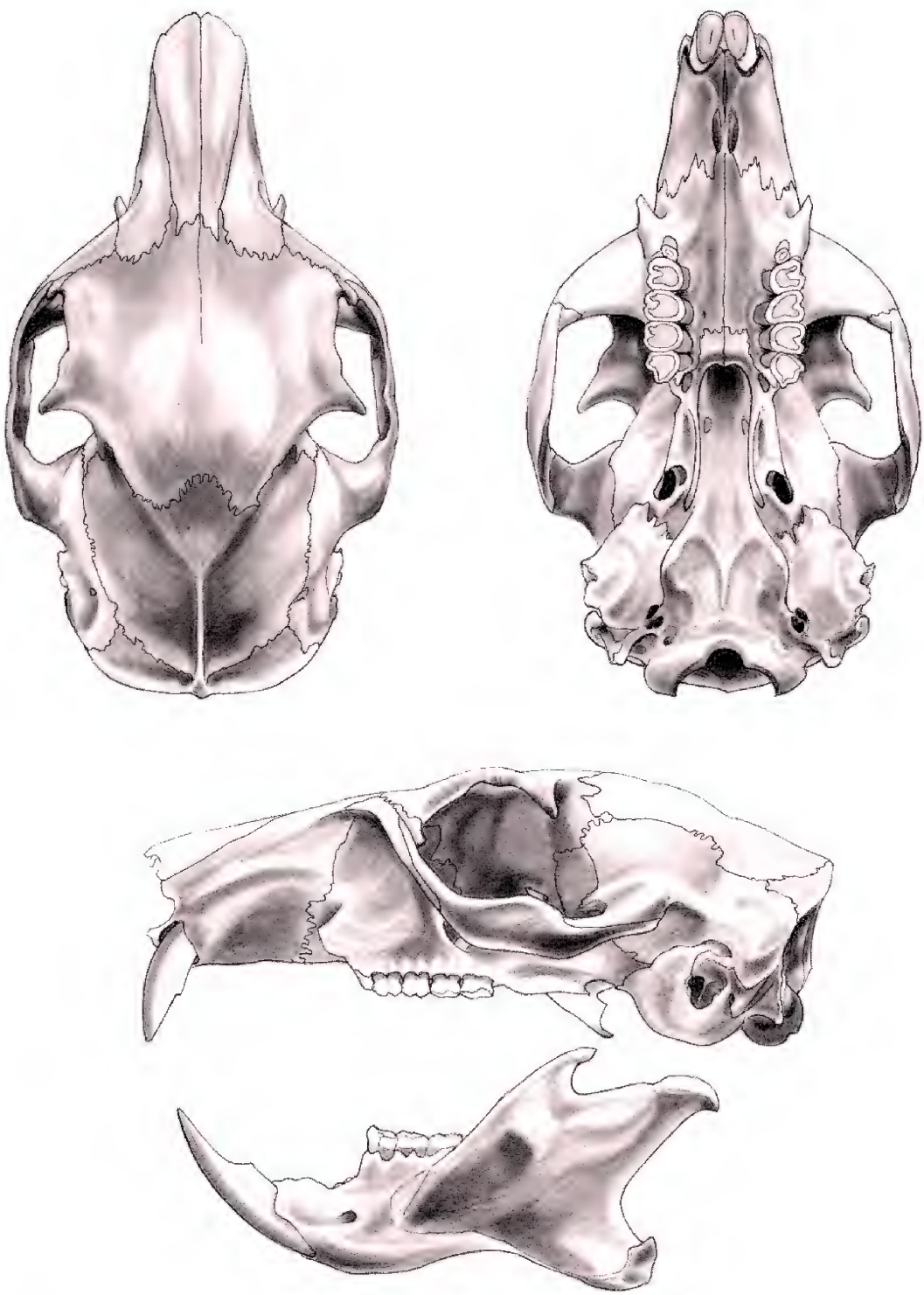

Fig. 6. Views of skull and dentary of an adult male *Rubrisciurus rubriventer* (AMNH 226053) from Kuala Navusu (30 m) in the central core of Sulawesi. Occipitonasal length = 67.4 mm.

TABLE 8
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Separate Population Samples of *Rubrisciurus rubriventer*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Northeastern peninsula $N = 2$	Northern peninsula $N = 5$	North-central region 1 $N = 18$	North-central region 2 $N = 19$	Southeastern peninsula $N = 5$	Combined samples $N = 49$
ONL	69.0 ± 1.27 (68.1–69.9)	67.9 ± 0.59 (67.5–68.9)	66.8 ± 1.75 (64.6–71.6)	66.9 ± 0.99 (65.2–68.4)	66.9 ± 1.55 (65.6–69.3)	67.0 ± 1.41 (64.6–71.6)
CBL	64.4 ± 1.06 (63.6–65.1)	62.9 ± 0.81 (62.0–64.1)	62.8 ± 1.50 (60.4–66.9)	62.8 ± 1.26 (59.9–64.7)	62.7 ± 1.45 (61.7–65.1)	62.8 ± 1.32 (59.9–66.9)
ZB	39.6 ± 1.27 (38.7–40.5)	38.3 ± 0.74 (37.4–39.4)	39.7 ± 0.68 (38.5–41.0)	39.3 ± 0.88 (38.1–41.2)	38.9 ± 0.64 (38.1–39.5)	39.3 ± 0.87 (37.4–41.2)
IB	22.8 ± 0.57 (22.4–23.2)	22.6 ± 1.23 (20.9–24.1)	22.3 ± 1.00 (20.5–24.3)	23.4 ± 0.90 (21.9–25.0)	22.0 ± 0.55 (21.3–22.8)	22.7 ± 1.06 (20.5–25.0)
LN	24.4 ± 0.57 (24.0–24.8)	22.9 ± 0.77 (21.7–23.8)	22.9 ± 1.24 (21.2–25.5)	22.8 ± 0.86 (21.1–24.7)	22.5 ± 1.50 (21.1–24.7)	22.9 ± 1.08 (21.1–25.5)
LR	31.7 ± 0.78 (31.1–32.2)	30.8 ± 0.30 (30.4–31.2)	29.9 ± 1.29 (27.7–33.0)	30.1 ± 0.62 (29.3–31.2)	30.9 ± 1.08 (29.5–32.5)	30.2 ± 1.04 (27.7–33.0)
BR	13.9 ± 0.14 (13.8–14.0)	13.5 ± 0.47 (13.1–14.3)	12.8 ± 0.74 (11.2–13.8)	12.8 ± 0.39 (12.1–13.4)	12.1 ± 0.44 (11.5–12.7)	12.8 ± 0.67 (11.2–14.3)
MB	26.8 ± 0.42 (26.5–27.1)	26.7 ± 0.50 (26.1–27.3)	27.3 ± 0.45 (26.3–27.9)	27.5 ± 0.61 (26.4–28.6)	27.2 ± 0.80 (26.3–28.2)	27.3 ± 0.59 (26.1–28.6)
HBC	20.1 ± 0.28 (19.9–20.3)	19.8 ± 1.04 (18.8–21.4)	20.4 ± 0.90 (19.3–22.2)	20.2 ± 0.55 (19.2–21.3)	20.5 ± 0.62 (20.0–21.5)	20.3 ± 0.75 (18.8–22.2)
LO	13.3 ± 0.28 (13.2–13.5)	13.5 ± 0.18 (13.2–13.6)	13.4 ± 0.50 (12.6–14.2)	13.3 ± 0.37 (12.6–13.8)	13.2 ± 0.30 (12.8–13.6)	13.4 ± 0.40 (12.6–14.2)
LD	16.8 ± 0.50 (16.4–17.1)	15.7 ± 0.53 (15.0–16.3)	15.8 ± 0.76 (14.8–17.5)	15.5 ± 0.76 (13.5–16.5)	15.4 ± 0.59 (14.4–15.8)	15.7 ± 0.74 (13.5–17.5)
LBP	20.5 ± 1.06 (19.7–21.2)	19.1 ± 0.26 (18.7–19.4)	19.2 ± 0.83 (18.2–21.1)	19.8 ± 0.64 (18.5–21.1)	19.1 ± 0.35 (18.5–19.4)	19.4 ± 0.76 (18.2–21.2)
PPL	26.1 ± 0.07 (26.0–26.1)	27.0 ± 0.46 (26.5–27.7)	26.6 ± 0.80 (25.3–28.2)	26.3 ± 0.66 (25.3–27.5)	27.1 ± 1.06 (26.5–29.0)	26.6 ± 0.77 (25.3–29.0)
BBP	15.3 ± 0.35 (15.0–15.5)	15.0 ± 0.27 (14.6–15.3)	14.7 ± 0.53 (13.7–15.6)	14.7 ± 0.46 (14.0–15.7)	14.0 ± 0.23 (13.7–14.3)	14.7 ± 0.52 (13.7–15.7)
LB	11.4 ± 0.35 11.1–11.6)	11.5 ± 0.29 (11.3–12.0)	11.1 ± 0.38 (10.5–11.9)	11.2 ± 0.58 (10.4–13.0)	11.4 ± 0.42 (10.9–12.0)	11.2 ± 0.47 10.4–13.0)
CLPMM	12.8 ± 1.06 (12.0–13.5)	13.0 ± 0.42 (12.5–13.5)	12.3 ± 0.59 (11.1–13.3)	12.8 ± 0.66 (11.3–14.0)	13.2 ± 0.27 (12.7–13.7)	12.7 ± 0.67 (11.1–14.0)

of the tooth row is a large notch or enclosed foramen (the posterior maxillary notch or foramen) that transmits the descending palatine vein (Wahlert, 1974). The vein passes through a notch in most specimens of *R. rubriventer* (ends of the notch are connected by cartilage, which is usually removed when the skull is cleaned), which is also typical in all the species of *Prosciurillus*. In a few examples of *R. rubriventer*, the opening is enclosed by bone forming a foramen (as shown in fig. 6), which is the typical configuration in both species of *Hyosciurus*.

Some of the other cranial traits seen in *R. rubriventer* are common to species of *Prosciurillus*, *Hyosciurus*, and most, but not all, other sciurids. Some examples are the proximal borders of the nasals, which lie anterior to the bordering premaxillary-maxillary sutures; moderate to prominent postorbital processes of the frontals; posterior border of the ventral zygomatic root at about the level of the second upper premolar; short and typically narrow incisive foramina contained entirely in the premaxillaries; a bony palate with a smooth ventral surface and penetrated by small postpalatal foramina at about the

level of the second upper molars; wide mesopterygoid fossa relative to skull size, its roof entirely osseous or showing slitlike sphenopalatine vacuities; relatively narrow pterygoid fossae bounded by a high lateral ridge; well developed hamular processes; moderately large ectotympanic bullae tightly attached to the basicranium; spacious postglenoid foramen just dorsad of the ectotympanic capsule; moderate-size coronoid process relative to overall outline of the dentary, large condyloid and angular processes, and deeply concave posterior border of the dentary.

Cranial and dental measurements for the population samples of *R. rubriventer* are summarized in table 8.

COMPARISONS: Members of the *Prosciurillus leucomus* and *P. murinus* groups as well as the species of *Hyosciurus* are all much smaller in body size than is *Rubrisciurus rubriventer* (table 3), none displays its bold and bright reddish, orange, brownish, and black patterning, and all females show three pairs of teats (see the appropriate accounts of species).

GEOGRAPHIC VARIATION: No additional scientific names have been attached to geographic samples of *R. rubriventer*, most likely a reflection of its generally uniform attributes associated with body size, pelage coloration and patterning, and cranial and dental dimensions among samples from the northern peninsula of Sulawesi, its central core, and southeastern arm. Sody (1949: 108) came close to naming a subspecies when he discussed the samples at MZB that he studied: a single specimen from Bumbulan on the northern peninsula and three from Palopo in the southern sector of the central core of Sulawesi (see gazetteer and fig. 5). Sody wrote that,

> It is only after much hesitation that I decided not to describe the Palopo animals as a new race. They are differing very strikingly from our Bumbulan specimen. Both forms have the same fulvous underside, arms and hands, legs and feet. But in the Bumbulan specimen the colour of the upperside is a mixture of black and fulvous-buff, in the Palopo series a mixture of brownish and buff. The general difference in colour is very large. And perhaps there also is a difference in the measurements. The reason why I do not separate the Palopo series, is, that it consists of old specimens (perhaps discoloured ?), whereas the Bumbulan specimen is from formaline.

Musser examined all four squirrels. The color contrast noted by Sody reflects primarily biological age of the specimens. The squirrel from Bumbulan is an adult covered in a full, richly pigmented adult coat. Of the three from Palopo, two are young and were captured as they were molting from juvenile into adult pelage, and the third is a juvenile completely covered in juvenile fur. Juveniles have thinner and shorter pelage showing slightly duller reddish hues along sides of the body, and duller fur over the head and back (the "mixture of brownish and buff") in some individuals, a conspicuous contrast with the thicker adult coat with its brilliant, darker hues.

Even among adults within a single geographic sample, or even in a sample from the same collection site, the fur over the head and back varies in color intensity among individuals. Some squirrels show a dark background speckled with buff (the buffy bands of the hairs are narrow, the black bands wider), but others have brighter fur in which the buffy speckling predominates (the buffy bands are wider, the black narrower); the brilliant reddish hues of the appendages, shoulders and thighs, and underparts are constant within and among population samples. Wear is also reflected in samples. Some older adults with worn pelage have darker upperparts because the fur has worn past the buffy or ochraceous distal bands and the remaining black bands of the hairs provide the prevalent tone.

All samples of *R. rubriventer*, from wherever they were collected on Sulawesi, exhibit similar pelage coloration and patterning over the body, whether adults or juveniles.

The possible difference in measurements suggested by Sody (1949: 108) can also be attributed to age. The adult from Bumbulan has a larger skull (greatest length = 68.5 mm) compared with the smaller skulls of the three younger squirrels from Palopo (greatest lengths are 64.0, 64.6, and 65.3 mm). The length of the skull of the Bumbulan animal falls within the range of variation we record within each of our geographic samples (see ONL in table 8). That measurement compatibility reflects the general geographic unifor-

mity of coat color and pattern among our samples of adult squirrels as well as overall size of skull and length of maxillary tooth rows. This cranial and dental dimensional variation within and among geographic samples is summarized in figure 7 where specimen scores representing five population samples of *R. rubriventer* (identified in table 1) are projected onto the first and second principal components extracted from principal-components analysis. The spread of scores along the first axis is primarily influenced by size, the larger and generally older adults spreading to the right, the smaller and usually younger adults towards the left. Covariation in most cranial variables—particularly length and breadth of rostrum, length of nasals, and lengths of diastema and bony palate—are the most influential in pushing scores along the first principal component; zygomatic breadth, mastoid breadth, and length of maxillary tooth row (PM4–M3) provide negligible impact (table 9).

No significant variation among measured cranial and dental dimensions that reflects altitudinal variation, particularly between lowland tropical evergreen rainforest habitats and lower montane forest, is apparent among our samples. Two sets of specimens provide examples. Scores shown in figure 7 representing specimens collected along Musser's transect in the central core of Sulawesi from Sungai Oha Kecil at 290 m to Gunung Kanino at 1418 m are identified by filled circles; slim arrows point to scores for the four squirrels collected in lower montane forest between 1274 and 1418 m on Gunung Kanino. Not only do most congregate within the cloud of points representing specimens from tropical lowland evergreen rain forest between Sungai Oha Kecil at 290 m and Tomado at 1000 m, but also within lowland samples from Kuala Navusu and Sungai Tolewonu (30–305 m; identified by asterisks) to the east of Gunung Kanino, and Masembo at 550 m (filled squares) in the southeastern peninsula. The other set originates from the southeastern peninsula and their specimen scores are indicated by filled squares. The square identified as Wawo at 50 m in tropical lowland evergreen rain forest rests next to the square for the specimen from Tanke Salokko at 1400 m in lower montane forest.

No discrete clouds of scores are present in the principal-components ordination that represents separate geographic regions. There are no unique constellations, for example, identifying samples from the northern peninsula, from the central core, or from the southeastern peninsula; all points derived from geographic samples are intermixed. Because each large sample ranges in age from young adults to old adults and includes males and females, the distribution of scores is also a reflection of age, possibly secondary sexual variation, and individual variation within an age class that is unrelated to age.

Four points at the right margin of the cloud in figure 7 require discussion. AMNH 224623, which is an especially large adult from Sungai Oha Kecil, is responsible for the score located farthest to the right in the ordination; most scores for other individuals from that collection site are nested within the primary cloud. Just to the left of AMNH 224623 is another point for a large adult from Sungai Oha Kecil, and that score is aligned with two scores identifying our only measured skulls from the northeastern limb of the northern peninsula. These two are also large adults, but we do not know if they are typical of the population in the northeast. We record more than a dozen specimens from that region (see gazetteer) but some are juveniles, some consist only of skins, and others have damaged skulls. A larger sample of adults with intact skulls needs to be studied to assess the range of cranial and dental morphometric variation within the northeastern peninsular population.

Our analysis of geographic variation in cranial and dental dimensions among samples available to us is rough. The results presented here should be tested by comparing larger samples of comparable age, supplemented by molecular data. What we convey here is the absence of significant differences in color pattern of the pelage, along with cranial and dental dimensions, among available samples of *R. rubriventer* from the different major geographic regions of Sulawesi. This large red squirrel looks the same wherever it is encountered on Sulawesi, a startling contrast to the variation associated

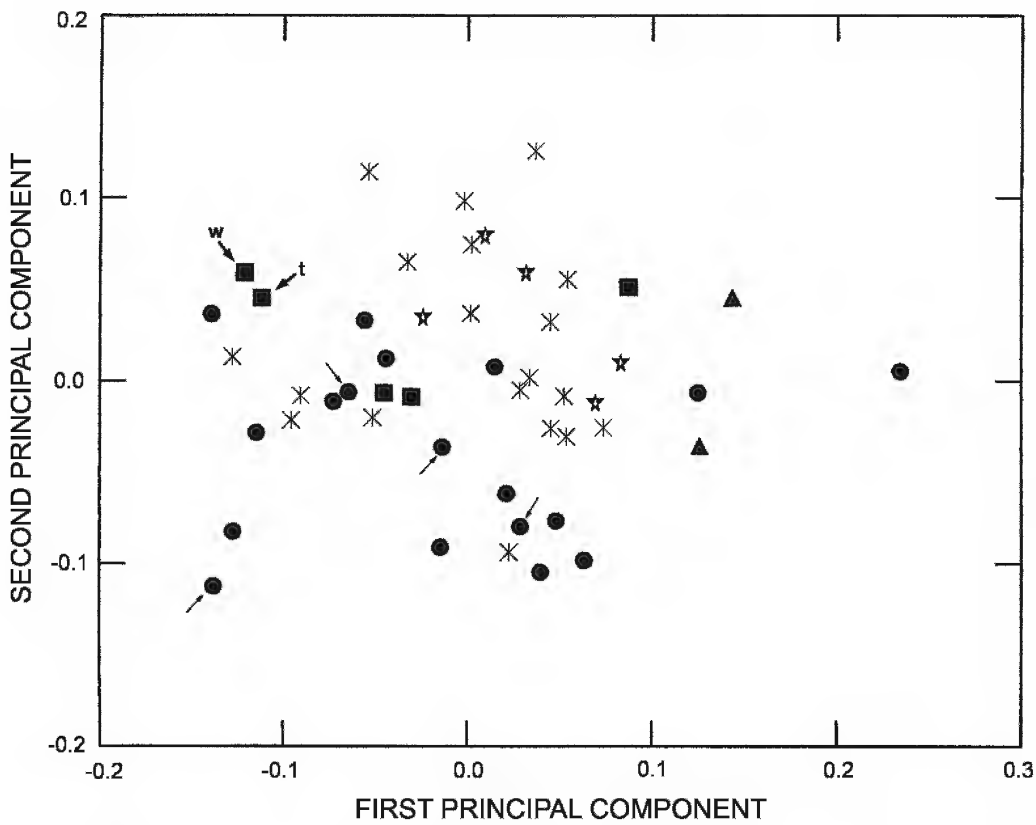

Fig. 7. Specimen scores representing five population samples of *Rubrisciurus rubriventer* projected onto the first and second principal components extracted from principal-components analysis. Symbols identifying samples are: filled triangle = northeastern peninsula (Rurukan, Temboan; $N = 2$); star = northern peninsula (Bumbulan, Ile-Ile; $N = 5$); filled circle = north-central region1 (Sungai Oha Kecil, Sungai Miu, Sungai Sadaunta, Tomado, Gunung Kanino, Kulawi; $N = 18$); asterisk = north-region 2 (Kuala Navusu, Sungai Tolewonu; $N = 19$); filled square = southeastern peninsula (Wawo, Masembo, Tanke Salokko; $N = 5$). The score located farthest to the right in the ordination represents AMNH 224623, an especially large adult from Sungai Oha Kecil. Delicate arrows identify scores of four specimens from Gunung Kanino collected in lower montane forest, 1274–1418 m. Lettered arrows indicate scores for the specimen from Wawo (w) collected on the coastal plain at 50 m in tropical lowland evergreen rain forest and the squirrel from the inland mountains at Tanke Salokko (t) at 1400 m taken in lower montane forest; both places are in the southeastern peninsula of Sulawesi. See table 9 for correlations and percent variance.

with fur color and patterns among geographic samples of the *Prosciurillus leucomus* complex (see those accounts).

ECOLOGY: *Rubrisciurus rubriventer* is diurnal, arboreal, and terrestrial. It nests in the forest understory and forages in the understory canopy and on the ground; Musser never saw any in the canopy layer or higher in the crowns of emergent trees. When squirrels were encountered, they were traveling through crowns forming the understory canopy or along the ground. Of the two squirrels briefly seen by Durden in the northeastern peninsula, one was in an understory tree and the other was on the ground. Musser trapped all his specimens on rotting tree trunks ("boles" to the botanists) lying on the forest floor, on tree or palm trunks lying across streams, on limbs of understory trees, and on the ground in scrub adjacent to tall forest (see summary of habitats at trapping sites in table 10, and the forest in fig. 8). Except for the specimen trapped in scrub, which was near tall forest, all sightings and

TABLE 9
Results of Principal-Components Analysis Contrasting Population Samples of *Rubrisciurus rubriventer*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 7.

Variable	PC1	PC2
ONL	0.018	0.000
CBL	0.018	−0.000
ZB	0.006	−0.004
IB	0.015	0.008
LN	0.039	−0.004
LR	0.025	0.004
BR	0.034	0.010
MB	0.004	−0.004
HBC	0.012	−0.006
LO	0.011	−0.007
LD	0.032	−0.022
LBP	0.022	0.008
PPL	0.013	0.000
BBP	0.010	0.005
LB	0.014	0.002
CLPMM	0.005	0.049
Eigenvalues	0.006	0.003
Percent variance	28.594	14.532

trapping records of *R. rubriventer* were in primary forest habitats on stream terraces, hillsides, and ridgetops.

From trapping records, the species is far more common than sightings would suggest—*Rubrisciurus* is quiet, wary, and easily startled. Although he spent every day in the forest checking traps and collecting botanical samples, Musser seldom saw *Rubrisciurus*; when he did, it was usually only as a reddish streak disappearing into the undergrowth or through the understory crowns. Once he saw two near camp at the Sungai Tokararu, one knocked over a live trap, the other scampered along a trunk on the ground, jumped off and poked around, then dashed into the undergrowth.

Two other sightings illustrate the squirrels' understory habits. On a hillside above the Sungai Tokararu, Musser had rebaited a rat trap and afterwards was sitting quietly on the dry leaf cover listening to sounds in the forest. He heard something upslope and after a few seconds a *Rubrisciurus* passed about 5 ft from him, progressing downhill in slow bounds alternating with an ambling walk. It held its tail out behind its back in a low arc. The squirrel did not react to Musser's presence, ambled by, looked around, then bounded down the slope over the litter and through the undergrowth until it was out of sight.

Musser enjoyed another rare encounter, this time in oak-chestnut forest on Gunung Kanino at 1500 m. He was sitting on a tree trunk and heard a squirrel move the dry leaf litter along the ridge, ambling and bounding along past him about 5 ft away. It bounced to a nearby chestnut, climbed over the roots and up one of the trunks to about 4 ft from the ground, straddled the trunk with its head down and its tail stretched out behind, looked downslope, uttered a few low growls, jumped to the ground, then bounded over the ridge and disappeared into the forest.

Rubrisciurus nests in tree cavities not far from the ground. Usma, one of Musser's helpers, described how he had once helped locate a nest. The villagers where he lived regularly used dogs to find the squirrels in the forest and then chase them to their nest. During one hunt, Usma located a nest in an old but still growing *pohon torode* (*Pterospermum celebicum*), with a trunk about 2.5 ft in diameter near the base. The base was hollow, forming an inverted cone-shaped cavity inside the trunk extending from the roots up for about 10 ft. The cavity was accessed by the squirrel through a hole about 4 ft from the ground. The original entrance to the cavity had been gnawed around the margins to form a larger opening. Wedged in the cavity between the opening and the roots was a large globular nest, about 1 ft in diameter with a single entrance, constructed entirely of the long, black sturdy fibers from a sugar palm (*Arenga pinnata*). The conformation of this nest, its construction material, and its placement, according to Usma and the few others we spoke to who were familiar with the squirrel's habits, were typical—large globular nests not far from the ground in cavities in the trunks of large trees.

In tropical lowland evergreen forest between the coast and about 1000 m, *Pterospermum celebicum* is common. Older trees contribute to the canopy; younger trees and saplings are familiar components of the understory, as well as in more open places in the forest. Musser never saw a tree with a basal diameter greater than 3 ft, and most of

Fig. 8. Habitat of *Rubrisciurus rubriventer* in tropical lowland evergreen rain forest at Kuala Navusu, 150 m. Two other species of tree squirrels live in the same forests: *Prosciurillus alstoni* prefers the upper canopy layer, and *P. murinus* forages through the understory trees. All three species were caught in traps set on top of tree trunks bridging streams, much like the trunk lying across the stream in the photograph. See table 2 for range of ambient temperatures recorded during the trapping period. Photographed in 1975.

those that large had already died and fallen to the ground. It grows along stream terraces, hillsides, and ridgetops. The sugar palm is found in the same forests all the way up to the lower limits of lower montane forest. Probably any large canopy-forming species that develop spacious cavities within the basal portion of the trunk could be used as a nest site. Strangler fig emergents in which the host tree has nearly or completely decayed are also likely candidates for protected nesting sites.

The diet of *Rubrisciurus rubriventer* consists of fruits, seeds, and insects. Remains of a variety of fruits and seeds were found in stomachs (tables 10, 57). We could identify figs (stomachs would be distended with chopped figs, pulpy endosperm, and small seeds); tan mash, possibly from pangi fruit; seeds from the monocot vine, *Rhaphidophora* sp.; fruit (the pulp) from trees in the Sapotaceae; seeds from the understory tree *pohon pangi* (*Pangium edule*); fruit from *pohon dongi* (*Dillenia serrata*), another understory tree; seeds of the ginger, *Etlingera celebica*; seeds from the magnolia *pohon uru* (*Elmerrillia ovalis*); and fruit of *Pandanus* spp. Caches of acorns from *Lithocarpus* could be seen in places throughout the forest but we never found anything in the stomachs of *Rubrisciurus* resembling acorn mash, and Musser never saw the red squirrel eating acorns that had fallen to the ground or were still attached to branches. Still, *Lithocarpus* fruit cannot be discounted as part of the diet.

Four kinds of fruit are regularly consumed by *Rubrisciurus*. Many species of fig form components of the forest habitats within the altitudinal range of the squirrel. Several species are limited to the understory, especially along banks of streams where ripe figs fall from the trees and litter the ground. Fruiting tall canopy and emergent species of strangler and other figs attract birds, canopy tree squirrels (*Prosciurillus*), and macaques during the day and fruit bats (Pteropidae) at night. The fruits not eaten in the crown of the tree eventually drop to the ground where they are accessible to *Rubrisciurus*, nocturnal rats, and other terrestrial mammals.

Pangium edule is common in the understory of forests along river terraces and hillsides in tropical lowland evergreen rain forest from the coastal lowlands to about 1100 m. The fruit is large (about 6 in. long and 3–5 in. wide) and woody, containing large and very hard seeds. Near camp on the Sungai Oha Kecil, Musser watched a *Rubrisciurus* climb a *pangi*, jump to a branch bearing fruit, bite the stem so the fruit crashed to the ground, then ran down the tree to disappear into the undergrowth because the squirrel had seen Musser. Remains of these large opened seeds are scattered over the stream terraces; here and there are caches beneath tree roots and rocks. The sound of the loud gnawing on the tough seed by the red squirrel travels through the forest, and often provides the only indication of the squirrel's presence.

The ginger is scattered through the lowland forests where it is most commonly seen in openings where secondary growth begins to cover old treefalls. When mature, the leafy stalks may be 12 ft high and the fruit forms huge clumps close to the ground—easily accessible to *Rubrisciurus*. *Rhaphidophora* sp., the monocot vine, is common in lowland rain forest. The fruit (5 × 1 in.) is composed of small seeds and an outside hard polygonal portion attached to a filamentous white woody base. Along streamside forest near Tomado, Musser startled a *Rubrisciurus* feeding on fruit from this vine, and partially eaten fruits were found at many places along the transect line.

With few exceptions, a predictable suite of insects was found in stomachs of many red squirrels: numerous remains of soldier and worker termites (head capsules, often still attached to partially digested bodies, bodies and legs, and sometimes intact termites), all representing Rhinotermitidae (Isoptera); legless larvae of beetles, Coleoptera (usually without head capsules, apparently the squirrel removes the head and ingests only the thorax and abdomen of the larva), which are common but not as abundant as the termites; and pupae of carpenter ants, occasionally with an adult ant (Formicidae, *Camponotus*). Some stomachs were packed with this combination of insect remains, always with the termites being the most abundant; other stomachs were distended with remains of the insect suite mixed with fruits and seeds. Rhinotermitid termites, legless beetle larvae and those with tiny and short legs, and pupae

TABLE 10

Summary of Habitat at Trapping Sites, Stomach Contents, and other Relevant Information for Specimens of *Rubrisciurus rubriventer* Collected by Musser in Central Sulawesi, 1973–1976

Collection locality, specimen number, elevation, and month and year of collection are included. Descriptions of the trapping sites and contents of stomachs, slightly edited, are from Musser's field journals (in mammalogy archives at AMNH). Six of the collection localities (Sungai Oha Kecil, Sungai Miu, Sungai Sadaunta, Tomado, Kuala Navusu, and Sungai Tolewonu) are in tropical lowland evergreen rain forest; lower montane rain forest describes the places on Gunung Kanino. With two exceptions, all squirrels were caught during the day in Conibear traps (rats taken in the same traps were caught during the night). Unless noted differently, trapping sites were in primary forest formations.

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
Sungai Oha Kecil 224621 (1758)	290	Aug. 1974	On small tree trunk over part of stream; caught early in the morning.
224622 (1789)	290	Aug. 1974	On trunk of understory tree growing over stream near spot where *Rubrisciurus* ASE 1758 was caught.
224623 (1893)	396	Aug. 1974	On small, smooth, wet and rotting trunk lying across stream about 1 ft from surface of water; sides of ravine above stream are steep, the terraces high above the stream.
Sungai Miu 224055 (1531)	350	Apr. 1974	On wet, bare, rotting trunk lying across stream in wet streamside forest; caught between 6:00 and 7:00 a.m.
224056 (1534)	350	Apr. 1974	On wet, rotting trunk lying on wet terrace in dense shrubby undergrowth next to stream.
Sungai Sadaunta 224052 (1336)	675	Feb. 1974	On decaying trunk lying in streamside forest and extending across Sungai Sadaunta to the opposite bank; caught about 8:00 a.m.
224041 (1414)	675	Feb. 1974	Five ft above ground on top of huge rotting trunk of giant canopy tree lying in dense understory of shrubs and ferns, crisscrossed by woody vines, in primary forest adjacent to stream. The tree squirrel *Prosciurillus murinus* and rat *Taeromys celebensis* were caught in same spot.
224054 (1459)	675	Mar. 1974	On rotting trunk lying in undergrowth of streamside forest.
224624 (1995)	762	Sept. 1974	On moss and fern-covered trunk lying across a dry ravine in hillside forest near camp; caught early in the morning. **Stomach**: empty.
224625 (2006)	793	Sept.1974	On small trunk lying across a ravine in tall hillside forest. **Stomach:** distended with remains of figs in which are mixed large and hard ginger seeds, numerous remains of worker and soldier rhinotermitid termites (head capsules, bodies, and intact termites), a few legless beetle larvae, an adult carpenter ant and a few carpenter ant pupae.
224626 (2033)	823	Sept. 1974	On wet, mossy trunk extending from one terrace of Sungai Sadaunta to the opposite terrace and resting just above water level on rocks in the stream; trunk would be inundated in high water. The rats *Maxomys hellwaldii* and *Bunomys* sp. were caught in same spot on different nights. **Stomach**: empty.
224627 (2350)	1006	Nov. 1974	On wet, moss-covered tree root growing across tributary creek in steep ravine. Caught rats (*Taeromys celebensis*, *Rattus marmosurus*, *Paruromys dominator* and *Bunomys* sp.) and *Prosciurillus murinus* just downstream on rotten trunk lying across stream.

TABLE 10
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
224628 (2354)	915	Nov. 1974	On limb of understory tree growing across ravine containing main upper tributary of the Sungai Sadaunta; base of the trunk is at edge of stream, with the trunk leaning over the water and its upper branches reclining on the opposite terrace. The main connecting limb (3–5 ft in. diameter) on which the trap was placed is mossy, and the moss is trampled, indicating frequent use; trap set about 7 ft from stream surface. The ground squirrel *Hyosciurus ileile*, the tree squirrels *Prosciurillus topapuensis* and *P. murinus*, and the arboreal rat *Rattus marmosurus* were taken in the same spot on different days. So three kinds of tree squirrels, one ground squirrel and at least one species of arboreal rat used the same living pathway as a bridge over the stream, the squirrels during the day, the rat at night.
224629 (2383)	777	Nov. 1974	On rotting, moss-covered trunk, partially covered by vines and ferns, lying across Sungai Sadaunta upstream from camp. A *Prosciurillus murinus* and the rat *Maxomys musschenbroeki* were trapped in same spot.
226839 (4318)	915	Mar. 1976	Caught between 5:30 and 6:00 a.m. at same spot on limb of understory tree where *Rubrisciurus* ASE 2354 and other rodents were trapped in 1974. **Stomach**: empty.
226840 (4388)	930	Mar. 1976	Caught during afternoon on large (2–3 ft diameter, 20 ft long) rotting trunk lying from high terrace, 10 ft above water, down across stream at an angle to other bank. Trunk is densely covered with ferns, monocot shrubs and smaller plants that form good cover for rodents using the trunk as a bridge. The rat *Echiothrix centrosa* was trapped in same spot. **Stomach**: partially full, remains of several kinds of fruit (skin, endosperm, seeds) including white, fibrous remains of seeds from the monocot vine *Rhaphidophora* sp.
Tomado 223466 (357)	1000	Aug. 1973	On rotting trunk lying across narrow stream in tall slightly disturbed primary forest. **Stomach**: partially full of mash from a soft fruit, ginger seeds and surrounding tissue, remains of fruit from the monocot vine *Rhaphidophora* sp, and a few remains of rhinotermitid soldier and worker termites.
223024 (358)	1000	Aug. 1973	On rotting trunk lying across stream in tall slightly disturbed forest; *Rubrisciurus* ASE 357 was trapped nearby.
223467 (378)	1000	Aug. 1973	Live trap on ground in dense shrubs and ferns at edge of meadow and second-growth forest behind rest house. **Stomach**: partially full of bait.
223025 (523)	1000	Aug. 1973	On large, rotting moss-covered trunk lying on ground deep in primary forest.
224057 (1608)	1000	May 1974	On rotten trunk lying across stream; scrub covers one bank, the opposite terrace supports tall forest. The rats *Maxomys hellwaldii* and *Rattus hoffmanni* were caught on same trunk.
Gunung Kanino 223552 (814)	1274	Nov. 1973	On living tree limb 3 ft from ground in dense, scrubby understory forest; caught in morning.
225488 (2520)	1402	Feb. 1975	On top of rotting trunk lying across narrow ravine; caught early in morning. **Stomach**: full of red fruit with small black seeds from *Pandanus*; still fresh, probably eaten just before caught.

TABLE 10
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
225489 (2533)	1418	Feb. 1975	On very mossy, rotting trunk lying across small tributary of Sungai Salubeka; the smaller stream courses along bottom of shallow ravine bounded by very wet and muddy slopes. The rat *Bunomys penitus* was taken at same spot. **Stomach**: remains of a large adult beetle; a bit of tan fruit; most of contents consist of a fibrous, bright lemon yellow fruit with small white seeds emitting a pungent, sweet, citrus-like odor (from a woody vine).
225490 (2462)	1418	Jan. 1975	On a pile of rotting trunk and limbs lying across small stream below camp. Two *Prosciurillus murinus* were trapped on same spot on different days. **Stomach**: full of pieces of white, orange and tan fruits; small hard white seeds; larger brown stony seeds; also bits of insect parts.
225491 (2476)	1512	Jan. 1975	Live-trap on ground placed within hollow base of rotten, moss-covered chestnut stump on ridge. The rat *Taeromys* sp. was taken in the same trap.
Kuala Navusu 226052 (3104)	31	Sept. 1975	On trunk (8 in. diameter) lying across ravine (5 ft wide) cutting down hillside behind camp. **Stomach**: full of mostly fruit and seeds (fig seeds from large understory fig, pieces of bright yellow fruit, and some triangular hard seeds and surrounding pulp), remains of large legless beetle larvae, and large margarodid scale insects, rhinotermitid worker and soldier termites (head capsules, some attached to partially digested bodies), and a few carpenter ant pupae; mostly the same combination of insects found in other *Rubrisciurus*.
226053 (3124)	31	Sept. 1975	On a decomposing palm trunk lying across stream near end of trapline. High, dense scrub covers stream banks in hillside forest partially thinned of canopy trees. A *Prosciurillus murinus* and the rat *Maxomys hellwaldii* were trapped at same spot. **Stomach**: partially full of pinkish tan mash with small cuboidal seeds from woody vine fruit, some remains of rhinotermitid termites, and many pupae of carpenter ants.
226054 (3141)	31	Sept. 1975	On rotting trunk (8 in. diameter) lying across stream below camp in old logging area, scrub and some secondary forest on either side of stream; caught another *Rubrisciurus* on a trunk lying across same stream about 100 ft downstream from where ASE 3141 was caught. **Stomach**: full of pink fruit pulp, small and hard cuboidal brown seeds; and long yellow seeds with orange tips from the monocot vine *Rhaphidophora* sp.
226055 (3177) 226056 (3229)	40	Sept. 1975	On rotting trunk (8 in. diameter) lying across steep tributary ravine; caught early in morning. One tree squirrel, *Prosciurillus alstoni*, was caught at the same spot on the previous day. **Stomach of ASE 3177**: full of fruit and seeds (brown fruit mash, some small cuboidal seeds, mostly remains of bright yellow fruit from woody vine) and purplish legless larval beetle abdomens. **Stomach of ASE 3229**: full of bright lemon-yellow fruit pulp (from woody vine).

TABLE 10
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226058 (3373)	61	Oct. 1975	On trunk (4 in. diameter) of living tree growing horizontally over a ravine; trunk is 5 ft above ravine bottom and extends 10 ft from one side of ravine to the other. A *Prosciurillus murinus* was taken in same place during a different day. **Stomach:** partially full of seeds from village ginger, unidentifiable fruit tissue, a few flat oblong seeds, many large and small legless beetle larvae, numerous remains of rhinotermitid worker and soldier termites, pieces of an adult beetle, including wings.
226057 (3555)	46	Nov. 1975	On branch of small, shrubby streamside tree growing across tributary draining west-facing slope, just up a few feet from main stream. Here ravine is 5 ft wide and 6–8 ft deep; good hillside forest.
226059 (3410)	122	Oct. 1975	Caught in morning on trunk (10 in. diameter) growing horizontal in understory; from base of slope the tree extends 3 ft over ground and across deep (15 ft) rocky ravine where crown ends about 10 ft off ground on other side of ravine; thick understory on both sides of ravine in tall hillside forest. Three *Prosciurillus alstoni* were taken in same trap on previous days. **Stomach:** nearly full with some tan fruit mash, but otherwise packed with legless coleopteran larval abdomens (30–50 mm long), rhinotermitid termite workers and soldiers, and a few carpenter ant pupae.
226060 (3617)	152	Nov. 1975	On long section of rotting trunk (10 in. diameter, 50 ft long) lying on sloping terrace above headwaters of main stream. Trunk lays about 2 ft off ground for most of its length. Intact tall hillside forest. **Stomach**: distended with Sapotaceae fruit; squirrel eats the pulp and green outer skin, but not the seed; could not find any trace of seeds, only pulp and skin. There is a large Nantu dropping fruit on east terrace and a tall *Madhuca* on west terrace, likely one of these is the source of fruit.
226061 (3655)	152	Nov. 1975	On rotting limb (8 in. wide, 8 ft long) that is extension of a long and large rotting trunk laying down the slope of the hill above a ravine. Tall primary hillside forest blankets area. **Stomach**: partially full of mostly one kind of fig (hard tiny black seeds, brown skin, thick rind) mixed with a few large (35–45 mm long) and small (5–10 mm) abdomens from legless beetle larvae, and some rhinotermitid worker and soldier termites.
226062 (3439)	244	Oct. 1975	On slender rotting trunk (diameter 6 in.) lying on steep dry slope. One side rests on ground; about 30 ft away, the other end rests on rotting trunk of a canopy tree that is laying down the slope. Forest is open here and adjacent understory is thin; a very old tree-fall cleared a large section that is only slowly being reforested. **Stomach**: partially full of bright yellow fruit mash.
Sungai Tolewonu 226532 (4016)	168	Jan. 1976	On rotting trunk lying across second large tributary; part of an old tree fall that is covered with a climbing ginger-like monocot, shrubs, ferns, and palm rosettes; about 6 ft above surface of water; caught in morning. A ground squirrel, *Hyosciurus ileile*, and a rat, *Maxomys hellwaldii*, were taken on same spot. **Stomach**: filled with mostly remains of fig (seeds and rind) mixed with several large and hard red seeds, a scattering of worker and soldier rhinotermitid termites, several legless beetle larva and buprestid beetle larvae, several large margarodid scale insects, and one macrolepidopteran caterpillar.

TABLE 10
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226534 (4017)	259	Jan. 1976	On wet, rotting, moss-covered trunk (40 ft long, 2 ft diameter) that is splintered into large sections and lying across stream and onto terrace and hillside; hillside forest of dense understory with scattered canopy trees. **Stomach**: nearly empty, small sections of fig and another kind of fruit mixed with chewed segments of legless coleopteran larval abdomens.
226535 (4039)	305	Jan. 1976	On decomposing trunk lying across branch of ravine in area of headwaters. The rat *Paruromys dominator* was caught in same place. **Stomach**: full of mostly pinkish-tan fruit mash and some bait.
226533 (4055)	229	Jan. 1976	On a 10-ft section of rotting trunk (10–12 in. diameter) covered with moss and resting across half of streambed 3 ft above water surface. Streambed is about 20 ft wide here between steep forested slopes and just at the top of the section of stream that is all rock. Caught about 8:00 a.m. **Stomach**: empty.
226526 (4154) 226528 (4189) 226539 (4220) 226530 (4257) 226531 (4259)	152	Feb. 1976	On rotting trunk of canopy tree (2 ft diameter, 50 ft long) bridging the main river about midway between first and second large tributaries. Trunk rests 4–7 ft above water level and is covered with thick moss on two sides and supports a few small shrubs, ferns, and palm seedlings scattered along the top of its length—not enough that provides any decent cover. Along the middle of trunk is a moss-free runway, about 5 in. wide that extends entire length (apparently a path frequently used by rodents to cross the river). On one side of the river is terrace forest, on the other side is steep, rocky moss-covered rocky slope that gives way above to hill forest on steep slopes. A *Prosciurillus murinus* and the rat *Paruromys dominator* were trapped at same spot. *Rubrisciurus* ASE 4220 was trapped in morning. **Stomach of ASE 4154**: empty. **Stomach of ASE 4189**: filled with same fruit mash as found in *Rubrisciurus* ASE 4158, along with small black seeds (probably fig), tiny brown seeds, large and hard oblong orange seeds, white fibrous seeds from the monocot vine *Rhaphidophora* sp., but no ginger seeds; a few small pieces of legless beetle larvae, numerous remains of rhinotermitid termite workers and soldiers, and a few carpenter ant pupae—same insect mixture found in other *Rubrisciurus* stomachs. **Stomach of ASE 4220**: half full with seeds from village-type ginger mixed with numerous rhinotermitid worker and soldier termites. **Stomach of ASE 4257**: half full with purple and tan fruit mash (with tiny hard black seeds and some large hard flat, oblong seeds), but most of contents consists of rhinotermitid termite workers and solders, and a few legless larval beetle abdomens. **Stomach of ASE 4259**: partially filled with hard brown seeds from village-type ginger in which the fruit is borne on stalks near ground—seeds are smaller than village ginger; also watery pulp in stomach is yellowish green.

TABLE 10
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226527 (4158)	165	Feb. 1976	On large rotting trunk of canopy tree (1.5 ft diameter, 45 ft long) bridging main river, extending from flat river terrace on one side to rocky hillside on the other bank, and about 5 ft above water level. Trunk is free of vegetation; a limb from an adjacent live tree parallels the dead trunk and its leafy branches provide partial cover over the top surface of dead tree. The tree squirrels *Prosciurillus alstoni* and *P. murinus* and the rat *Maxomys hellwaldii* were taken on same trunk. **Stomach**: half full of rubbery fruit pulp and three kinds of seeds (large seeds from village ginger, elongate flat seeds, tiny black seeds), shredded white fibrous seeds from the monocot vine *Rhaphidophora* sp.; also some remains of rhinotermitid termite workers and soldiers.

of carpenter ants are part of a community found only in dead and rotting wood, especially pieces partially covered by leaf litter and soil (D. Grimaldi, personal commun., 2009). Musser often encountered deeply excavated sections of wet and rotting tree trunks and limbs lying on the forest floor as well as the erect bases of rotting tree and palm trunks. He dug into several undisturbed sections and found adult Coleoptera, legless beetle larvae, and sometimes termites. *Rubrisciurus rubriventer* travels and forages on the ground as well as in the understory canopy; on the ground, it clearly digs into rotting wood and exposes the insects.

The squirrel must also pick insects off leaf litter, tree trunks, and limbs in the understory canopy. One stomach contained a large adult beetle mixed with fruit mash. Another held buprestid beetle larvae, a macrolepidopteran caterpillar, and large margarodid scale insects mixed with the usual combination of termites and legless beetle larvae. Adult beetles are on the ground and in the trees; buprestid larvae are found beneath rotting bark, both on trunks and limbs decaying on the forest floor and on lower limbs and trunks of living trees; the scale insects occur on the surface of the bark, usually on the trunk or in tree crowns, some occur on wood on or near the ground.

The skull of *Rubrisciurus* is large and sturdy, with strong procumbent incisors, a long rostrum relative to size of the skull, only slight cranial flexion, prominent temporal ridges that combine to form a pronounced sagittal crest reflecting significant temporal musculature, a large and sturdy platform for the insertion of the superficial masseter, and a large, robust mandible (see fig. 6). That combination of traits among Sulawesi's endemic tree squirrels—*Rubrisciurus* and species of *Prosciurillus* (compare the skull of *Rubrisciurus* in fig. 6 with those of *Prosciurillus* depicted in figs. 12–14)—is restricted to *Rubrisciurus*. This morphology is well adapted to gnawing open large and tough woody nuts, such as those from *pangi*. It is also structurally suitable for excavating rotten tree limbs, trunks, and stumps. The wood is soft and pulpy and no special adaptations to claws would be necessary for the job. But in addition to front claws, the squirrel may depend on its large and strong incisors, especially the procumbent uppers (see fig. 6) to dig into the decaying wood. Also, the rostrum, relatively long compared with the relatively very short rostrum of the other species of Sulawesi tree squirrels, may contain a greater area of nasal epithelium providing the enhanced olfactory acuity necessary for detecting insects in decaying wood. Musser did not see a red squirrel actually digging into decaying parts of old treefalls, but did surprise one squirrel that had been sniffing about a small rotting tree trunk on the ground.

In contrast to *Rubrisciurus rubriventer*, the other Sulawesi tree squirrels—*Prosciurillus*

alstoni, *P. topapuensis*, and *P. murinus* (and the other members of the *P. leucomus* and *P. murinus* groups)—have a very short rostrum compared to skull length, strong cranial flection, faint temporal ridging, and no sagittal crests; and also the anteroventral corner of the ventral zygomatic root is relatively thinner and the outer osseous surface only slightly roughened to accommodate the insertion of the superficial masseter (see figs. 12–14). The morphology suggests a diet of softer foods than those described for *Rubrisciurus*, and that locating certain dietary elements by olfaction may not be as important in these squirrels as in *Rubrisciurus*. All three species of *Prosciurillus* introduced above consume soft fruits (figs are an example) as well as insects (table 57). Contents of stomachs held no indication that tough nuts were taken, such as those from *pangi* and oaks. The insects in the stomachs examined are macrolepidopteran and geometrid caterpillars along with beetles, scale insects, and cockroaches (most of which are gleaned from surfaces of foliage and bark); and buprestid beetle larvae dug from beneath bark (see ecology accounts for the different species). Contents of stomachs also point to arboreal termites in Termitidae as part of their diet. Nests of these insects are fastened to limbs in tree crowns and easily scratched open by the squirrels, causing the termites to pour out of the nest onto the branch to quickly become easy prey. The suite of insects living in rotting wood—terrestrial termites in Rhinotermitidae, legless beetle larvae, and carpenter ant pupae—sought by *Rubrisciurus* was not found in the any of the stomachs we examined from *Prosciurillus*.

Rubrisciurus rubriventer's large body size (500–800 g) and long legs, its bright red coloration and bushy tail, its wary and quiet nature, its habits of foraging and traveling through tree crowns in the understory layer and along the ground, and nesting in the base of hollow trees in tropical rainforest habitats are a combination seen in two other species, both in a different phylogenetic lineage (Sciurinae) than that of *Rubrisciurus* (Nannosciurinae), and occurring on another continent. The northern Amazon red squirrel, *Sciurus igniventris* (500–900 g), and southern Amazon red squirrel, *Sciurus spadiceus* (600–650 g) are endemic to tropical rainforest habitats in the Amazon Basin of South America (Emmons and Feer, 1990: 167–168). Each is red, large-bodied, long-legged, and bushy-tailed (see pl. 19 in Emmons and Feer, 1990). Both are wary, quiet, and travel in the understory canopy or along the ground; neither one travels through the upper canopy of the forest. Palm nuts along with other kinds of large seeds and fruit form their diets, and both squirrels can be located in the forest by the sounds of their gnawing on the tough palm nuts. Insects, however, have not been recorded as part of their diets (although we are not aware of any study examining contents of stomachs). There is apparently an ecological niche in New and Old World tropical forests centering on understory habitats occupied by diurnal tree squirrels sharing a close similarity in morphology, diet, and other ecological parameters, but with different evolutionary histories rooted in widely separate lineages within Sciuridae.

ECTOPARASITES: In addition to the sucking louse *Hoplopleura rubrisciuri*, n. sp. (see description in a following section), the flea *Medwayella rubrisciurae* (Siphonaptera, Pygiopsyllidae) has been recorded from vouchers of *Rubrisciurus rubriventer* collected at Tomado and Sungai Sadaunta in the west-central region of Sulawesi's central core (Durden and Beaucournu, 2006). Another species of flea, *Macrostylophora theresae* (Ceratophyllidae), parasitizes three species of endemic Sulawesian murid rodents (*Bunomys fratrorum*, *Paruromys dominator*, and *Rattus xanthurus*). However, Durden and Beaucournu (2006: 224) speculated that *Rubrisciurus rubriventer* might be the true host because other members of this flea genus are ectoparasites of squirrels, especially larger-bodied tree squirrels, throughout Southeast Asia. *Rubrisciurus rubriventer* is also parasitized by immature stages (larvae and/or nymphs) of hard ticks (Acari, Ixodoidea, Ixodidae) belonging to four different genera: *Amblyomma* sp., *Dermacentor* sp., *Haemaphysalis* sp., and *Ixodes* sp. (Durden et al., 2008). *Amblyomma* sp. and *Haemaphysalis* sp. have also been collected from *Hyosciurus heinrichi*, and *Dermacentor* sp. and *Haemaphysalis* sp. from *Hyosciurus ileile* (table 56). Collectively, in addition to the

squirrel hosts, the four tick genera have been collected from a suite of other mammal hosts living in Sulawesi: shrews (the endemic *Crocidura* sp. and *Crocidura elongate*, and the commensal *Suncus murinus*), pigs (*Sus celebensis*, an endemic, and *S. scrofa*, feral domestic), rusa (*Rusa timorensis*, nonnative), water buffalo (*Bubalus bubalis*, nonnative), humans, domestic dog (nonnative), nine species of endemic murid rodents (*Bunomys chrysocomus* and *B. fratrorum*; *Margaretamys beccari*; *Echiothrix centrosa*; *Maxomys hellwaldii*, *M. musschenbroekii*, and *M. wattsi*; *Paruromys dominator*; *Taeromys* sp.; *Rattus hoffmanni*, *R. xanthurus*, and *R. marmosurus*), and four nonnative rats (*Mus musculus*; *Rattus tanezumi*, *R. argentiventer*, and *R. exulans*; Durden et al., 2008). Ectoparasitic laelapid mites were recovered from *R. rubriventer* pelt AMNH 101316 which was collected at Wawo, Pegunungan Mekongga, in southeastern Sulawesi at an elevation of 50 m in 1932.

SYMPATRY: The range of *R. rubriventer* on mainland Sulawesi overlaps that of all species of *Prosciurillus*, except for *P. abstrusus*, as well as both species of *Hyosciurus* (table 6). Along his transect in the northern portion of central Sulawesi, Musser trapped *R. rubriventer* in the same traplines, and sometimes in the same traps, as *P. topapuensis*, *P. alstoni*, *P. murinus*, and *H. ileile* (table 10).

SYNONYMS: None.

Prosciurillus Ellerman, 1947

The generic name *Prosciurillus* was generated after Ellerman had measured the orbit of hundreds of European and Asiatic squirrel skulls and discovered that species of the Indomalayan pygmy squirrels in *Nannosciurus*, the Sulawesian ground squirrel *Hyosciurus*, and Sulawesian small-bodied tree squirrel *murinus* all had a short orbit compared to all other squirrel taxa examined, less than one-fourth of the occipitonasal length. He (Ellerman, 1947: 259) proposed "*Prosciurillus* as a new genus for *Sciurus murinus*" and compared it to the South American pygmy squirrel *Sciurillus*, with which it has no close phylogenetic alliance as would be documented decades into the future (Moore, 1959; Mercer and Roth, 2003). Eleven years later, Moore (1958) redefined *Prosciurillus*, describing several anatomical traits associated with the skull that he thought to be diagnostic in addition to the relatively short orbit, and expanded the contents of the genus to include the Sulawesian *leucomus* (and presumably all the taxa associated with it, although not explicitly stated by Moore; see table 11).

Moore's (1959: 176) expanded report of relationships among living squirrels, which contained the results of his survey of cranial characters in the Sciurinae, brought together *Prosciurillus* with the Sulawesian *Rubrisciurus* and *Hyosciurus*, as well as the Sundaic-Philippine *Exilisciurus* in the subtribe Hyosciurina of the tribe Callosciurini. Except for *Exilisciurus*, Moore's hypothesis of phylogenetic relationships for *Prosciurillus* has been unambiguously supported by analyses of the nuclear IRBP and mitochondrial 12S and 16S ribosomal DNA used by Mercer and Roth (2003) to recover a squirrel phylogeny that included a monophyletic group containing *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* separate from a cladistic cluster formed by *Callosciurus*, *Sundasciurus*, and their relatives. Within the Sulawesian clade, the species of tree squirrels in *Prosciurillus* are more closely related to *Rubrisciurus* than to the morphologically divergent ground squirrels in *Hyosciurus*. The phylogram of relationships generated by Mercer and Roth excludes the species of pygmy squirrels in *Exilisciurus* from the Sulawesian clade (see introductory discussion in the account of *Rubrisciurus*).

The short orbit (indicated by the lacrimal and posterior margin of the zygomatic plate situated even with the second upper molar) and lack of transbullar septa in more than 50% of large samples (see Moore, 1959: 163) are the strongest cranial traits distinguishing *Prosciurillus* from most genera of Nannosciurinae. But among the Sulawesi endemics, a short orbit is also common to *Rubrisciurus* and *Hyosciurus*, as is either the complete absence or low frequency of occurrence of transbullar septa. All three genera also possess third premolars and exhibit parallel upper tooth rows. Otherwise, *Prosciurillus* is easily distinguished from *Rubrisciurus* and

Hyosciurus by the following combination of traits (see comparative measurements summarized in table 3, color plates of live poses in figs. 9 and 10, and compare skulls illustrated in figs. 6, 12–14, 36, and 37): **(1)** short face and much smaller in body size (table 2), the two smaller-bodied species often referred to as pygmy tree squirrels (but still much larger than the species in *Nannosciurus* and *Exilisciurus*, the true pygmy or dwarf tree squirrels); **(2)** upperpart dark brown or chestnut brown and without pattern, or lacking pattern except for black ear tufts, or possessing black ear tufts with nape patches behind ears, or exhibiting black ear tufts and prominent black middorsal stripe from neck to base of tail (no ear tufts, nape patches, or dorsal stripe in *Hyosciurus*; reddish orange fore-legs and feet, shoulders, thighs, and hind legs and feet in *Rubrisciurus* combined with black ear tufts); **(3)** underparts reddish orange to ochraceous, brownish gray, or dark gray washed with pale buff or silver (white or cream in *Hyosciurus*, reddish orange in *Rubrisciurus*; **(4)** hind foot short and broad, the typical configuration in tree squirrels, claws short and strongly recurved (hind foot long and slender in *Hyosciurus*, claws very long and only slightly curved); **(5)** tail slightly shorter than length of head and body (half the length of head and body in *Hyosciurus*; table 3); **(6)** three pairs of teats, one postaxillary and two inguinal (two inguinal pairs in *Rubrisciurus*; one abdominal pair and two inguinal pairs in *Hyosciurus*); **(7)** skull small and gracile with marked cranial flexion (robust, with strikingly reduced cranial flexion in *Rubrisciurus* and *Hyosciurus*); **(8)** rostrum short and wide, nasals and premaxillaries not forming a tube projecting beyond faces of upper incisors (rostrum moderately long in *Rubrisciurus*, very long in *Hyosciurus* where nasals and premaxillaries form a tube projecting anterior to faces of incisors); **(9)** nasals much shorter than length of frontals (53%–66% of length of frontals) and shorter than width of interorbital region (nasals as long as frontals or only slightly shorter, and nasals longer than width of the interorbital region in *Rubrisciurus* and *Hyosciurus*); **(10)** temporal ridges barely evident and reach occiput without coalescing to form a sagittal crest (stronger temporal ridges that combine to form sagittal crests in *Rubrisciurus* and *Hyosciurus*); **(11)** postorbital processes of the frontals about even with anterior wall of the braincase (well anterior to the braincase in *Rubrisciurus*); **(12)** anterior opening of the infraorbital canal lies slightly posterior to the premaxillary-maxillary suture and is concealed behind bony flange slightly or markedly projecting from ventral root of the zygoma, the anteroventral corner of the flange slightly thickened and marked on outer surface by a barely perceptible roughened elliptical area for insertion of the superficial masseter; **(13)** posterior border of bony palate located anterior to backs of the tooth rows, at about middle of each third upper molar (even with end of tooth rows or slightly caudad of tooth rows in *Hyosciurus*); **(14)** descending palatine vein transmitted through a notch (posterior maxillary notch; a foramen instead of a notch occurs in about 5% of all total skulls examined) at the posterolateral margin of bony palate just caudad and slightly medial to end of tooth row (vein is enclosed by bone forming a foramen in *Hyosciurus*); **(15)** pterygoid fossa narrow and deep, its lateral margin forming a high ridge—Moore's (1959) "ectopterygoid ridge"(lateral margin outlined by a low, inconspicuous ridge in *Hyosciurus*); **(16)** upper incisors proodont (procumbent), projecting forward (orthodont, oriented at right angle to rostrum in *Hyosciurus*); **(17)** upper third molar roughly triangular in occlusal view, about as long as it is wide (oblong in *Rubrisciurus*, much shorter than wide). Traits shared with *Rubrisciurus* and *Hyosciurus* are summarized in the diagnoses for those genera.

We provide accounts for the seven species of *Prosciurillus*, which are divided into two groups based on contrasts in coat color and patterning combined with physical body size. Squirrels of medium build (length of head and body = 155–195 mm) exhibiting a combination of dorsal and ventral pelage coloration along with patterns associated with ear tufts, nape patches, and middorsal back striping comprise the *P. leucomus* group (*P. leucomus*, *P. alstoni*, *P. weberi*, *P. topapuensis*, and *P. rosenbergii*). Small-size squirrels (length of head and body = 102–150 mm) with dark brown upperparts,

TABLE 11
Allocation of Scientific Names Associated with Species in the *Prosciurillus leucomus* Group as Presented in Primary Checklists of Mammals from 1940 to the Present
The combination of generic and specific names as originally proposed is listed in their published chronological order. See the accounts of species for names of authors and dates of publication.

Original combination (in *Sciurus* or *Callosciurus*)	Ellerman, 1940 (in *Callosciurus*)	Laurie and Hill, 1954 (in *Callosciurus*)	Corbet and Hill, 1992 (in *Prosciurillus*)	Thorington and Hoffmann, 2005 (in *Prosciurillus*)	Present report (in *Prosciurillus*)
S. leucomus	*C. leucomus leucomus*	*C. leucomus leucomus*	*P. leucomus leucomus*	*P. leucomus leucomus*	*P. leucomus*
S. rosenbergii	*C. rosenbergii*	*C. leucomus rosenbergii*	*P. leucomus rosenbergii*	*P. rosenbergii*	*P. rosenbergii*
S. alstoni	—	—	*P. leucomus*?	—	*P. alstoni*
S. weberi	*C. weberi*	*C. leucomus weberi*	*P. weberi*	*P. weberi*	*P. weberi*
S. tonkeanus	*C. tonkeanus*	*C. leucomus tonkeanus*	*P. leucomus*	*P. leucomus tonkeanus*	*P. alstoni*
S. tingahi	*C. tingahi*	*C. leucomus tingahi*	*P. leucomus*	*P. rosenbergii*	*P. rosenbergii*
S. leucomus occidentalis	*C. leucomus occidentalis*	*C. leucomus occidentalis*	*P. leucomus occidentalis*	*P. leucomus occidentalis*	*P. leucomus*
S. sarasinorum	*C. sarasinorum*	*C. sarasinorum*	*P. leucomus sarasinorum*	*P. leucomus*	*P. alstoni*
S. topapuensis	*C. topapuensis*	*C. leucomus topapuensis*	*P. leucomus*	*P. leucomus*	*P. topapuensis*
S. mowewensis	*C. mowewensis*	*C. mowewensis*	*P. leucomus*	*P. leucomus*	*P. alstoni*
S. elbertae	*C. elbertae*	*C. elbertae*	*P. leucomus*	*P. leucomus*	*P. alstoni*
C. leucomus hirsutus	—	*C. leucomus occidentalis*	*P. leucomus hirsutus*	*P. leucomus hirsutus*	*P. topapuensis*

slightly contrasting underparts, and generally without ear, nape or back displays (except for white fur on backs of the ears in *P. abstrusus*) form the *P. murinus* group (*P. murinus* and *P. abstrusus*).

The *Prosciurillus leucomus* Group

The first-named member of this assemblage, *P. leucomus*, was described by Müller and Schlegel in 1844. From then until now, 11 scientific names have been attached to the group, most of them described as species of *Sciurus* (table 11; also see Roux, 1910: 520). By 1940, Ellerman (1940: 375), in his compendium on the families and genera of living rodents, had transferred the taxa from *Sciurus* to *Callosciurus* and recognized a "*leucomus* Group" containing nine species. During the years to follow, the taxa associated with the *leucomus* cluster were shifted from *Callosciurus* to *Prosciurillus* (Moore, 1959; Corbet and Hill, 1992; Hoffmann et al., 1993; Thorington and Hoffmann, 2005) and the number of species recognized in primary checklists of mammals dropped to four (Laurie and Hill, 1954: 93), then two (Corbet and Hill, 1992: 304; Hoffmann et al., 1993: 436), and eventually was elevated to three (Nowak, 1999: 1270; Thorington and Hoffmann, 2005: 785). We recognize five species (table 11).

Our hypotheses of species-boundaries are based on results from our qualitative study of variation in coat-color patterns and quantitative analyses of morphometric variation in cranial and dental traits, bolstered by insights from geographic and altitudinal distributions determined from collection localities of voucher specimens. Different chromatic patterns and pelage traits (variation in coloration of upperparts and underparts, presence or absence of ear tufts and when present their coloration and degree of expression, and presence or absence of nape patches and middorsal stripes) and geographic distributions of the various chromatic combinations

Abh. Ber. K. Zool. Anthr. Ethn. Mus. Dresden 1896/7 Nr. 6
Meyer, Säugethiere Celebes-Philippinen Taf. X
1 Sciurus tonkeanus A.B.Meyer c. 3/4 n. Gr.
2 Sciurus leucomus Müll. Schl. unter 1/3 n. Gr.
3 Sciurus rosenbergi Jent. c. 1/3 n. Gr.
4 Sciurus tingahi A.B.Meyer c. 2/5 n. Gr.

Fig. 9. Reproduction of Meyer's (1896) color plate showing "*Sciurus leucomus*" (= *Prosciurillus leucomus*) at the top, "*Sciurus tonkeanus*" (= *Prosciurillus alstoni*) in the center, "*Sciurus rosenbergii*" (= *Prosciurillus rosenbergii*) on the bottom right and "*Sciurus tingahi*" (also = *Prosciurillus rosenbergii*) at bottom left.

provide the primary diagnosis for each species (summarized in table 12). Morphometric distinctions parallel the chromatic contrasts but are less conspicuous compared with the striking variation in color patterns and appreciated only with measurements from large samples. All the species are similar in body size and cranial and dental dimensions (tables 15–17). They are intermediate in physical size (130–210 g) between the larger-bodied Indomalayan tree squirrels *Callosciurus prevostii* (250–500 g) and *Sundasciurus hippurus* (260–365 g) and the smaller-bodied tree squirrels *Callosciurus adamsi* (115–154 g) and *Sundasciurus lowii* (60–120 g), and more similar to the common *Callosciurus notatus*

Abh. Ber. K. Zool. Anthr. Ethn. Mus. Dresden 1898/9 Nr. 7
Meyer: Säugethiere Celebes II. Taf. V
Sciurus sarasinorum A. B. Meyer
nat. Grösse u. 1/2 nat. Grösse

Fig. 10. Reproduction of Meyer's (1898) color plate of "*Sciurus sarasinorum*" (= *Prosciurillus alstoni*). The top portrait was rendered from the specimen collected at Mapane, the bottom from the squirrel obtained at Usu (see gazetteer and the account of *P. alstoni*).

(150–315 g) and *C. nigrovittatus* (147–257 g); see Medway (1969) and Payne et al. (1985). Among the Sulawesi endemics, *Prosciurillus leucomus* and its four allies are each physically much smaller than *Rubrisciurus rubriventer* but larger than each member of the *Prosciurillus murinus* group (table 3).

Definitions for three of the five species are enhanced by their sucking lice parasites. Each of the three species of squirrels that are defined by color pattern of fur, morphometric traits, and explicit geographic boundaries support a unique species of *Hoplopleura* (see accounts of the sucking lice). Unfortunately, we did not recover lice were from pelts of the other two species (*P. rosenbergii* and *P. weberi*).

GAZETTEER AND SPECIMENS EXAMINED: Collection localities for the 177 examples of

P. leucomus, the 107 specimens of *P. alstoni*, the eight specimens of *P. weberi*, the 78 specimens of *P. topapuensis*, the 39 examples of *P. rosenbergii*, and the single subfossil of *Prosciurillus* sp. studied are listed below. The number preceding each locality in the gazetteers for *P. leucomus*, *P. alstoni*, *P. weberi*, *P. topapuensis*, and *P.* sp. keys to a symbol on the map in figure 11. The distribution of *P. rosenbergii* on islands forming Kepulauan Sangir is featured on the map in figure 28.

Prosciurillus leucomus

1. **Likupang**, 01°41′N, 125°03′E, coastal plain near sea level: USNM 216786–92; SNSD B3431; ZMB 92614.
2. **Teteamoet** (several miles southeast of Likupang; see Raven's brief description of the place in Miller, 1917: 29), 01°40′N, 125°05′E (estimated from Raven's map), on coastal plain near sea level: USNM 216769–216785.
3. **Pulau Lembeh**, 01°26′N, 125°13′E (elevation of collection site is not recorded but highest point of the island is 447 m): Meyer (1896: 25) reported two specimens from this island. One (SNSD B3081) resides in the collection at Dresden, the other was sold (C. Stefen, in litt., 2008).
4. **Manado** (also spelled "Menado"), 01°30′N, 124°50′E, coastal plain near sea level: ANSP 14156; MZB 6235–37; RMNH 13343 (paralectotype of *Sciurus leucomus*; specimen "*a*" in Jentink's catalog, 1888: 24), specimens "*c*" and "*q*" in Jentink's (1888: 24–25) catalog, RMNH 24434, and an uncataloged specimen; ZMA 19.867–19.871; ZMB 4119.
5. **Lotta**, 01°25′N, 124°49′E, coastal plain near sea level: ZMB 92616. Meyer (1896: 25) reported a specimen from Lotta.
6. **Ajermadidi** (also spelled Airmadidi), 01°26′N, 124°58′E, 200–300 m (estimated from Sheet NA 51-12): USNM 217823.
7. **Rurukan**, 01°21′N, 124°52′E, 900 m: AMNH 196569, 196563–68, 196570–73; ANSP14157; BMNH 1899.12.9.80, 1899.12.9.81, 1899.12.9.82; FMNH 8329; ZMB 13829/13929, 84939, 84940.
7. **Tonsealama** (also known as "Tonsea"), 01°19′N, 124°55′E, 600–700 m (estimated from Sheet NA 51-12): BMNH 1940.670, 1940.671 ("Tonsea"); MZB 6229–33.
8. **Kema**, 01°22′N, 125°03′E, coastal plain near sea level: RMNH 13344 (lectotype of *Sciurus leucomus*; specimen "b" in Jentink's catalog, 1888: 24).
9. **Tondano**, 01°19′N, 124°54′E, 600–700 m (estimated from Sheet NA 51-12): MZB 6234.
10. **Gunung Masarang**, 01°19′N, 124°51′E, 3500 ft (1067 m): ANSP 14154, 14155; BMNH 1897.1.2.15, 1897.1.2.16; SNSD B3430.
11. **Tomohon**, 01°19′N, 124°49′E, 700–800 m (estimated from Sheet NA 51-12): BMNH 1899.10.1.5; NMB 4246/1105, 9544/1197.
12. **Temboan** (on Kuala Kalait, "is a new clearing of eight houses and lies from Mt. Sapoetan south, 55° west and about six miles from Loboe," wrote Raven in his field journal, 1916: 3 (in mammal division library at USNM), 01°03′N, 124°33′E (estimated from Raven's map), 500 m (estimated from Sheet NA 51-12): USNM 217822, 217825, 217826.
13. **Amurang**, 01°11′N, 124°35′E, on coastal plain near sea level: MZB 1500, 1501; SNSD B261, B622.
14. **Tulabolo** ("Toelabello" in Jentink's [1888: 25] catalog), 00°31′N, 123°16′E, 760 ft (230 m; see Fooden [1969: 137] for details): RMNH: specimens "*i*" and "*j*" in Jentink's (1888: 25) catalog (paralectotypes of *Sciurus leucomus occidentalis*).
15. **Gorontalo**, 00°31′N, 123°03′E, coastal plain near sea level: SNSD B168 (holotype of *Sciurus leucomus occidentalis*). **"Panybie"**: RMNH: specimen "*l*" in Jentink's (1888: 25) catalog. "**Modélido**": RMNH: specimen "*m*" in Jentink's (1888: 25) catalog. (Specimens "*l*" and "*m*" are paralectotypes of *Sciurus leucomus occidentalis*.) The last two localities are near Gorontalo (see Meyer, 1896: 26) but we don't know exactly where.
16. **Limboto** (also spelled Limbotto), northwest shore of Danau Limboto, 00°37′N/122°57′E, 0–100 m (estimated from Sheet NA51-14): RMNH: specimen "*p*" in Jentink's (1888: 25) catalog (paralectotype of *Sciurus leucomus occidentalis*).
17. **Bumbulan**, 00°29′N, 122°04′E, coastal plain near sea level: AMNH 152916–20, 152922–31, 152933–37; MZB 6239–42, 6246–48.
18. **Paguat** (also spelled Pagowat), 00°26′N, 121°54′E, coastal plain near sea level: RMNH specimen "*k*" in Jentink's (1888: 25) catalog (paralectotype of *Sciurus leucomus* and *Sciurus leucomus occidentalis*).
19. **Sungai Paleleh** ("I went inland about four or five miles over the mountains and made camp at the edge of the Paleleh River, which is a small brook ... with steep mountains or hills on all sides" [Raven, in Miller, 1915: 23]), 00°59′N, 121°49′E (estimated from Raven's map), 700 m (estimated from Sheet NA 51-14): USNM 200270–73.
20. **Matinan** ("Matinang" is an older spelling), 01°05′N, 121°42′E (for village near coast;

TABLE 12
Some Characteristics Distinguishing Members of the *Prosciurillus leucomus* Group
Listed are pelage traits, extremes (mm) in ranges of selected external and cranial measurements, and weight (g) summarized from tables 14–16; ranges of collection elevations and general geographic distributions are included.

Feature	*P. leucomus*	*P. alstoni*	*P. weberi*	*P. topapuensis*	*P. rosenbergii*
Ear tufts	Black and prominent	White and prominent; absent from some specimens	Black and prominent	Black: ranges from prominent to faint	Not present
Nape patches behind ears	Expansive, white to whitish buff or whitish gray; or paler and smaller; not present on a few specimens	Not present	Not present	Not present	Not present
Upperparts of head and body	Dark brown with buffy, orange and black highlights	Dark brown with buffy, orange and black highlights	Dark brown with buffy, orange and black highlights	Brown with buffy and black highlights	Rich, dark chestnut- brown
Mid-dorsal stripe	Not present	Not present	Broad and black, extending from neck to base of tail	Not present	Not present
Underparts of head and body	Reddish orange through orange-red to ochraceous	Dark, rich red to reddish brown (approaching chestnut) most frequent; some are reddish orange; overall typically more intensely pigmented than *leucomus*	Reddish orange	Dark gray lightly washed with pale buff or ochraceous, some tinted silver	Dark brownish gray to brownish buff
LHB	165–188	157–195	187	155–190	190
LT	140–190	135–180	142	120–175	180
LT/LHB (%)	95–98	89–99	89	82–91	95
LHF	43–47	40–48	43	38–50	42
WT	—	135–210	—	130–210	—
ONL	44.1–47.6	40.7–46.5	42.7–46.7	42.0–47.2	—
CLPMM	7.1–8.0	7.3–8.4	6.5–7.2	6.8–8.0	7.3–7.9
Elevation (m)	Coastal plain to 1700	Coastal plain to 1200	Coastal plain	350–2800	?
Distribution	Northern peninsula mainland; Pulau Lembeh	East-central peninsula, eastern sector of central core, southeastern peninsula; Pulau Buton, Pulau Kabaena	Southern part of central core	Mountains in western section of central core	Kepulauan Sangihe

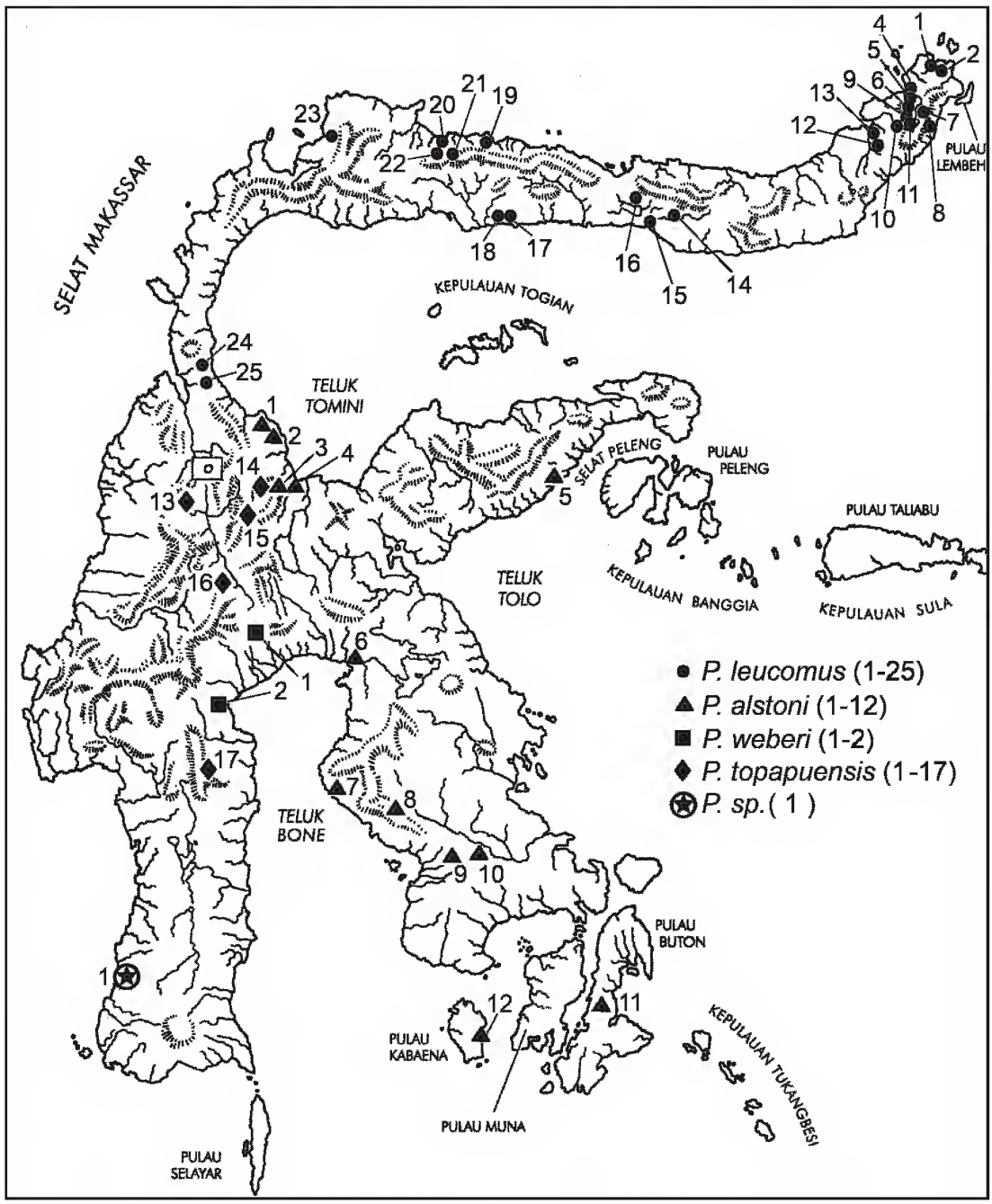

Fig. 11. Collection localities for samples of four species in the *Prosciurillus leucomus* group: *P. leucomus*, *P. alstoni*, *P. weberi*, and *P. topapuensis*. The collection site for *Prosciurillus* sp., which is represented by a subfossil fragment, is also indicated. Distribution of the fifth member, *P. rosenbergii*, in Kepulauan Sangihe is portrayed on the map in figure 28. Numbers key to localities described in the gazetteer where specimens are also identified by museum initials and catalog numbers. The inset map, right (rectangle in larger map, above), contains collection sites (1–12) for *P. topapuensis* scattered along Musser's transect from the Sungai Miu to Gunung Nokilalaki. The dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and tropical lower montane forest.

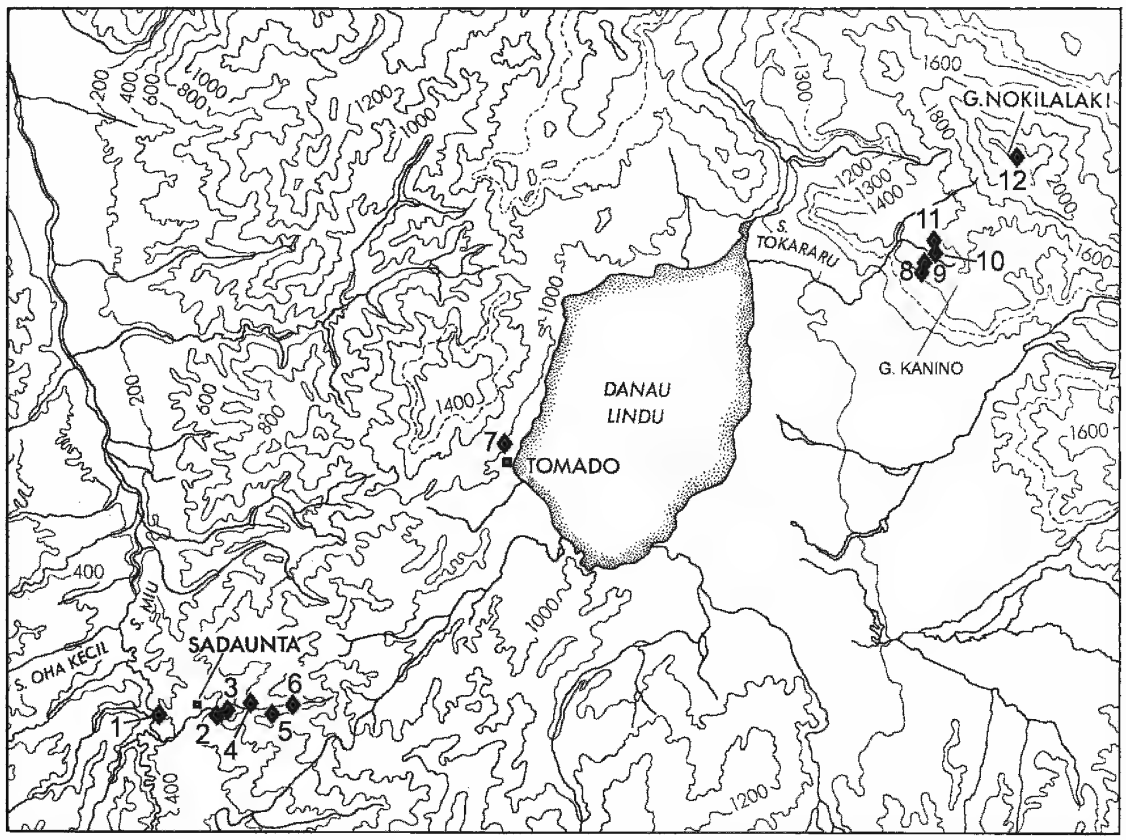

Fig. 11. *Continued.*

specimens came from south of village at 600 m in foothills of Pegunungan Paleleh): AMNH 196547–49.

21. **Gunung Matinan** (also spelled "Matinang"), part of the broader Pegunungan Paleleh in the northwestern part of the northern peninsula, 1000 m: NMB 1198 (skin)/9543 (skull), paralectotype of *Sciurus leucomus occidentalis*.
22. **Gunung Ile-Ile**, 00°58′N, 121°48′E (one of the high places in the more expansive Pegunungan Peleleh traversing the northwestern part of the northern peninsula): AMNH 196559–62 (500 m), 196550–58 (1700 m).
23. **Tolitoli**, 01°03′N, 120°49′E (estimated from Raven's map), on coastal plain near sea level: USNM 200274.
24. **Labuan Sore** (spelled "Laboea Sore" on specimen labels and "Laboean Sore" on Raven's map), on east coast just north of Marantate, about midway between Towera and Toboli, 00°37′S, 120°03′E (estimated from Raven's map; see Bynum et al., 1997, who discussed this collection locality), 200 m (estimated from Sheet SA 51–1): USNM 218074–77.
25. **Bumbarujaba** (spelled "Bumbaroedjaba" on specimen labels), on highway crossing the peninsula between Tawaeli and Toboli, 00°43′S, 120°04′E (estimated from Raven's map), 915 m (according to Riley, 1924: 2): USNM 218708, 218709.

Specimens from the northern peninsula we studied but did not map are listed here. RMNH specimens "*d–h*," "*n*," and "*o*" ("Célèbes") are entered in Jentink's (1888: 24–25) catalog. (Jentink's skin "*d*" was collected by S.C.J.W. van Musschenbroek, who was "resident" [= district officer] in Manado during 1875–76; see Van Steenis-Kruseman [1950: 378]. This animal therefore must be from NE Celebes. Other material that was collected by van musschenbroek includes the rats *Maxomys musschenbroekii* and *M. hellwaldii*, and the civet *Macrogalidia musschenbroekii*, all obtained near Manado. C. Smeenk, personal commun., 2010.) Six further paralectotypes of *Sciurus*

leucomus are in RMNH: 39392 and 39393 (skeletons "*a*" and "*b*" in Jentink's [1887: 191] osteological catalog), and RMNH 39395–98 (skulls "*c–f*" in Jentink's [1887: 191] osteological catalog, all collected by E.A. Forsten in 1841 from "Célèbes" [= NE Celebes]. Three uncataloged skins from "N. Celebes" and a skin from "Minahasa, Celebes" are also housed in RMNH. SNSD B2745 and ZMB 92379, 92380, and 92615 are from "Main, Minahasa." "Minahasa, N. Celebes" is the only locality designation for NMB 9546/1104 and SNSD B2745. Seven specimens at BMNH (1849.3.2.7, 1886.6.26.1, 1943.239–1943.243) are from "Celebes."

Prosciurillus alstoni

1. Malakosa, **Kuala Navusu**, 00°58′S, 120°27′E (estimated from Sheet SA 51-1): 100 ft (30 m), AMNH 226076–81; 125 ft (38 m), AMNH 226082; 130 ft (40 m), AMNH 226083–85; 150 ft (46 m), AMNH 226086; 175 ft (53 m), AMNH 226087; 400 ft (122 m), AMNH 226088–96; 450 ft (137 m), AMNH 226097–99; 500 ft (152 m), AMNH 226100; 750 ft (229 m), AMNH 226101.
2. Tolai, **Sungai Tolewonu**, 01°04′S, 120°27′E (estimated from Sheet SA 50-8): 400 ft (122 m), AMNH 226510–12; 500 ft (152 m), AMNH 226513, 226514; 540 ft (165 m), AMNH 226515; 650 ft (198 m), AMNH 226516, 226517; 800 ft (244 m), AMNH 226518; 950 ft (290 m), AMNH 226519; 1000 ft (305 m), AMNH 226520, 226521; 1050 ft (320 m), AMNH 226522; 1100 ft (335 m), AMNH 226523, 226525; 1200 ft (366 m), AMNH 226524.
3. **Pinedapa**, 01°25′S, 120°35′E (estimated from Raven's map), 100 ft (31 m): USNM 219511–21, 219523–40.
4. **Mapane**, 01°26′S, 120°40′E, near sea level: SNSD B3826 (lectotype of *Sciurus sarasinorum*).
5. **Tonkean**, near Sinorang, 01°24′S, 122°30′E, 0–100 m (see Fooden, 1969: 137: SNSD B3178 (lectotype of *Sciurus tonkeanus*), B3179–B3186 (paralectotypes of *tonkeanus*; see Feiler, 1999: 407).
6. **Usu** ("Oesoe" on old maps; also spelled "Ussu"), 02°36′S, 121°06′E, coastal plain at the northern end of Teluk Bone, 0–100 m: NMB 1199 (skin), 8080 (skull), paralectotype of *Sciurus sarasinorum*.
7. **Wawo**, on the plain between the coast and western foothills of Pegunungan Mekongga (also spelled "Mengkoka"), 03°41′S, 121°02′E, 50 m: AMNH 101329–39, 101347.
8. Pegunungan Mekongga, **Masembo**, which is southeast of Wawo and the highest place in the southern portion of Pegunungan Mekongga (see maps and discussion in Heinrich [1932] and Stresemann [1940]) 03°35′S, 121°15′E (for the Pegunungan), 550 m: AMNH 101340–46.
9. **Mowewe**, 04°10′S, 121°52′E, approximately 500 m: NMB 1626 (skin), 4243 (skull), lectotype of *Sciurus mowewensis*. Sungai Ahua: NMB 1627 (skin), 4244 (skull), paralectotype of *Sciurus mowewensis*.
10. **Lalolei** (spelled "Lalolis" on specimen tags and some maps), 03°57′S, 122°03′E, 300 m: AMNH 101325–28.
11. **Pulau Buton**, off the coast of the southeast peninsula, topographic relief ranges from sea level to 1190 m: MZB 6250, 6251. We do not know where on the island these two squirrels were collected and simply placed a dot randomly within the island's outline. Sody (1949: 107) examined the pair and noted that "These two animals have been a long time in the Museum [MZB], until lately stuffed, now made to study skins. On the glass of the case, in which they were exhibited, was an indication: '*Sciurus tonkeanus* Meyer. Boeton, Mohari leg.' I am not able to say much more."
12. **Pulau Kabaena**, off the coast of the southeast peninsula, topographic relief ranges from sea level to 1570 m: SMF 721 (holotype of *Sciurus elbertae*), 4878 (both specimens, skulls only, were kindly examined for us by G. Storch). Schwarz (1911: 639) identified the type locality as "Eempuhu, East Kabaëna." We could not find Eempuhu on any maps or in any gazetteers consulted and simply placed a dot on the eastern side of the island.

Prosciurillus weberi

1. **Masamba**, 02°34′S, 120°19′E, coastal plain, 0–100 m: MZB 6252, 6253. 2. **Palopo** ("near Palopo"), 03°01′S, 120°13′E, 0–100 m: BMNH 94.7.4.6 (a skin only, which is one of the *specimens* upon which Jentink's [1890] original description of *Sciurus weberi* is based, and is a paralectotype); MZB 6254, 6256; RMNH 13342 (lectotype of *Sciurus weberi*); ZMA 11.327 and 11.328 (each is a paralectotype of *Sciurus weberi*).

Prosciurillus topapuensis

1. Valley of Sungai Miu, **Sungai Miu** (right side), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 350 m: AMNH 224042.
2. Valley of Sungai Miu, **Sungai Sadaunta** (also spelled "Sidaonta" or Sidaunta"; tributary on right side of Sungai Miu), 01°23′S,

119°58′E (estimated from Sheet SA 50-8), 675 m: AMNH 224041.
3. **Sungai Sadaunta**, 2500 ft (762 m): AMNH 224581; 2700 ft (824 m), AMNH 224582.
4. **Sungai Sadaunta**, 2850 ft (869 m): AMNH 224584, 224585.
5. **Sungai Sadaunta**: 2900 ft (884 m), AMNH 224599, 224611.
6. **Sungai Sadaunta**: 3000 ft (915 m), AMNH 224586–88; 3050 ft (930 m), AMNH 226835.
7. Valley of Danau Lindu, **Tomado** (a village on western shore of Danau Lindu), 01°19′S, 120°03′E (estimated from Sheet SA 5-8), 1000 m: AMNH 226932 (caught at 1140 m).
8. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 4600 ft (1402 m): AMNH 225501, 225502; 4650 ft (1418 m), AMNH 225504.
9. **Gunung Kanino**, 4700 ft (1433 m): AMNH 225503.
10. **Gunung Kanino**, 4800 ft (1463 m): AMNH 223532–35; 4900 ft (1509 m), AMNH 225505.
11. **Gunung Kanino**, 5050 ft (1540 m): AMNH 225506, 225507.
12. **Gunung Nokilalaki**, 01°13′S, 120°08′E, 7520 ft (2293 m): AMNH 223531.
13. **Gunung Lehio**, 01°33′S, 119°53′E, at or above 6000 ft (1829 m): USNM 218714–18, 218720–23.
14. **Rano Rano**, 01°30′S, 120°28′E, 6000 ft (1829 m): USNM 219483, 219484, 219486, 219487, 219490–501, 219503.
15. **Besoa**, 01°44′S, 120°13′E (for "Besoa District," HOUSND, 1944); see description in gazetteer for *Rubrisciurus rubriventer* collection localities: USNM 219485, 219488, 219489, 219502. Along the **"Lindoe Trail"**: USNM 218719.
16. **Gunung Topapu**, approximately 02°S, 120°15′E (estimated from a copy of the map used by P. and F. Sarasin, the collectors of the specimen), 1550 m: NMB 1628 (skin), 4245 (skull).
17. **Pegunungan Latimojong**, 03°30′S, 121°23′E, 2200 m: AMNH 196534–44; 2800 m, AMNH 196545, 196546.

The following specimens were studied but the place where they were caught is not mapped.

Central Core, **Tamalanti**, 3300 ft (1006 m): BMNH 1940.691e, 1940.691f, 40.691g (holotype of *Callosciurus leucomus hirsutus*), 1940.691h–1940.691j. Laurie and Hill (1954: 156) noted that Tamalanti is a "Plantation between Rantekaroa [02°50′S, 119°50′E] and Koelawi [01°27′S, 119°59′E]," which was also the only information Musser and Paula Jenkins found when they searched through fieldnotes and other documents at BMNH.

Prosciurillus sp.

1. **Ulu Leang I** (a cave about 40 km northeast of Ujung Pandang in the Maros region; see map and description in Glover, 1976), 0–100 m: AMNH 269955 (subfossil fragment of a right dentary; see table 33 and fig. 29).

Prosciurillus rosenbergii

We examined all the specimens in RMNH and ZMT, and most from SNSD. Feiler's (1990) informative report documenting historical material in SNSD collected from the Kepulauan Sangihe did not tie individual specimens by catalog number to different island provenances, but Clara Stefen kindly provided that information for the few SNSD specimens we did not examine.

Kepulauan Sangihe, **Pulau Sangihe** (also spelled "Sangir"), 03°33′N, 125°30′E; BMNH 1876.10.21.4; FMNH 31846; RMNH 13351–53 (specimens "*a–c*" in Jentink's [1888: 23] catalog; paralectotypes of *Sciurus Rosenbergii*), RMNH 13354 (specimen "*d*" in Jentink's [1888: 24] catalog; paralectotype of *Sciurus rosenbergii*) and RMNH specimens "*m*" and "*n*" in Jentink's (1888: 24) catalog; SNSD 2551–53, 2559; ZMB 5128, 84973, 92377. Pulau Sangihe, **Tabukan**: SNSD 499, 500. (Chris Smeenk provided this note: one should be careful here. Although the specimens obtained by von Rosenberg are labeled "Sanghir", in his manuscript notes von Rosenberg uses that name for the entire archipelago, and it cannot now be ascertained whether his material came indeed, all or part of it, from the main island P. Sangihe. Jentink's specimen "*d*" collected by Hoedt seems more reliable in this respect, as Hoedt labeled all his other specimens "Siao". The specimens obtained from the dealer G.A. Frank again, are labeled "Sangir" without further specification.)

Kepulauan Sangihe, **Pulau Siau** (also spelled "Siao"), 02°49′N, 125°23′E: RMNH 13355–61 (specimens "*e–k*" in Jentink's [1888: 24] catalog; paralectotypes of *Sciurus Rosenbergii*), RMNH 13362 specimen "l" in Jentink's [1888: 24] catalog; lectotype of *Sciurus Rosenbergii*); SNSD 323, 2554, 2555–58, 2560, 2561.

Kepulauan Sangihe, **Pulau Tahulandang** (also spelled "Tahoelandang," "Tagulandang," and "Tangulandang"), 02°21′N, 125°25′E: SNSD B2842 (lectotype of *Sciurus tingahi*), B2843 and B2844 (paralectotypes of *Sciurus tingahi*).

Kepulauan Sangihe, **Pulau Ruang** (also spelled "Roeang"), Gunung Api, 02°18′N, 125°22′E for Pulau Ruang: SNSD 2847, 2848, 2850, 2851 (paralectotypes of *Sciurus tingahi*).

Prosciurillus leucomus (Müller and Schlegel, 1844)

Sciurus leucomus Müller and Schlegel, 1844: 87.
Sciurus leucomus occidentalis Meyer, 1898: 2.

LECTOTYPE AND TYPE LOCALITY: The lectotype of *Prosciurillus leucomus* is an adult male (RMNH 13344, specimen "*b*" in Jentink's, [1888: 24] catalog) obtained by E.A. Forsten in 1840 from "Célèbes, Kéma." It consists of a skin mounted in a live pose and a slightly damaged skull (extracted from the mount after Jentink's tenure at Leiden). The nasals are missing, there is a large hole in the right frontal bone, one upper molar and one maxillary premolar are missing, and four upper molars and one premaxillary molar are present but have fallen out of their alveoli; the mandible is intact and all teeth are present. Dental and some cranial measurements are listed in table 13.

Specimen "*b*" was one of eight specimens cataloged as types (= syntypes) by Jentink (1887: 191, 1888: 24). Following Chris Smeenk's suggestion (in litt., 2008), we select specimen "*b*" as the lectotype, following the rules promulgated in Article 74.1 of the Code (ICZN, 1999: 82). The other seven become paralectotypes: **(1)** specimen "*a*" (Jentink, 1888: 24), RMNH 13343, an adult female, a skin mounted in live pose and extracted skull collected by E.A. Forsten on April 6, 1840, from "Célèbes, Ménado"; **(2)** skeleton "*a*" (Jentink, 1887: 191), RMNH 39392, an adult skull and postcranial skeleton, sex unknown, collected by E.A. Forsten in 1841 from "Célèbes"; **(3)** skeleton "*b*" (Jentink, 1887: 191), RMNH 39393, a juvenile skull and postcranial skeleton, sex unknown, collected by E.A. Forsten in 1841 from "Célèbes"; **(4)** skull "*c*" (Jentink, 1887: 191), RMNH 39395, an adult damaged cranium with missing dentaries, sex unknown, collected by E.A. Forsten in 1841 from "Célèbes"; **(5)** skull "*d*" (Jentink, 1887: 191), RMNH 39396, an adult skull with incomplete right dentary, sex unknown, collected by E.A. Forsten in 1841 from "Célèbes"; **(6)** skull "*e*" (Jentink, 1887: 191), an adult damaged skull, sex unknown, collected by E.A. Forsten in 1841 from "Célèbes"; and **(7)** skull "*f*" (Jentink, 1887: 191), a damaged skull, sex unknown, collected by E.A. Forsten in 1841 from "Célèbes." Chris Smeenk (in his unpublished catalog of types at Leiden) has also included specimen "*k*" (Jentink, 1888: 25), RMNH 39394, in the type series, an adult male, mounted in live pose, no skull present, collected from "Célèbes, Pagowat." Although no further details are given, this can only be the "*Sciurus*" collected by E.A. Forsten from Pagowat (= Paguat) during November 5–12, 1841, as mentioned in his diary, a copy of which (in an unknown hand) is preserved in the archives of the Leiden Museum (Chris Smeenk, in litt., 2008).

The type locality is Kema, 01°22′N, 125°03′E, near sea level on the coastal plain of the northeastern peninsula (locality 8 in gazetteer and map in figure 11), Propinsi Sulawesi Utara, Indonesia.

Chris Smeenk provided us with pages dealing with the Sulawesi squirrels from his manuscript version of the "Type-specimens of recent mammals in the National Museum of Natural History, Leiden," and it is pertinent here to reproduce his remarks regarding the lectotypes and paralectotypes of "*Sciurus leucomus*":

> Müller & Schlegel (1844) do not state how many specimens they had before them. The skulls of Jentink's skins *a* and *b* (RMNH 13343 and 13344) were extracted at a later date. Jentink (1887) also lists as types two skeletons and four separate skulls collected by Forsten. Although Müller & Schlegel do not mention skeletal material, they had these specimens available when writing their descriptions, and hence they are included in the type series here.
>
> Forsten arrived in Manado in Northeast Celebes on 22 March 1840; on 15 April he made his headquarters at Tondano, from where he explored Minahasa (Manado) District in the northeastern tip of the island. He arrived back in Manado on 24 April 1841, departed from Kema on 14 June, and landed in Ternate on 19 June. On 9 September 1841 he proceeded to Gorontalo in NE Celebes, where he arrived on

TABLE 13

Age, Sex, and External, Cranial, and Dental Measurements (mm) for Holotypes Associated with *Prosciurillus topapuensis* (includes *hirsutus*), *Prosciurillus weberi*, and *Prosciurillus leucomus* (includes *occidentalis*)

The taxa were originally described as members of either *Sciurus* or *Callosciurus*.

Variable	*Sciurus topapuensis* NMB 4245[a]	*Callosciurus leucomus hirsutus* BMNH 40.691[b]	*Sciurus weberi* RMNH 13442[c]	*Sciurus leucomus* RMNH 13344[c]	*Sciurus leucomus occidentalis* SNSD B168[d]
Type	holotype	holotype	lectotype	lectotype	holotype
Age	young adult	adult	adult	adult	adult
Sex	female	male	female	male	?
LHB	150	185	187	—	—
LT	95	115	142	—	—
LHF	41 [44]	36	43	—	—
LE	13	15	17	—	—
ONL	45.1	—	45.3	—	—
CBL	—	36.9	40.1	41.3	—
ZB	—	25.5	27.0	29.2	29.1
IB	15.2	14.8	16.4	17.8	20.0
LN	12.9	12.4	12.5	—	13.1
LR	20.3	18.7	20.4	—	23.0
BR	9.1	8.6	9.5	9.4	—
MB	18.8	19.3	19.0	19.7	—
HBC	15.6	15.5	15.2	15.6	—
LO	—	—	10.5	10.0	—
LD	9.1	8.8	10.1	9.0	10.1
LBP	13.1	11.6	12.9	13.5	—
PPL	—	15.8	18.4	17.4	—
BBP	9.5	9.6	10.0	11.1	10.7
LB	7.9	7.5	7.8	7.3	—
CLPMM	7.5	7.4	7.2	—	8.0

[a]Values for lengths of head and body, tail, hind foot, and ear are from Roux's (1910: 518) description. His value for hind foot length excludes the claws; adding 3 mm for claws produces the figure in brackets. Ear length is likely from base to crown of the pinna, not from notch to crown. Loïc Costeur, at NMB, measured the skull and teeth, and provided us with color images of both skull and skin.

[b]Hayman (1945: 577–578) provided these external measurements, but with this explanation: "All measurements of the new form are taken from the relaxed skins before making up. It seems necessary to make considerable allowances for stretching in skinning, since the head and body figures prove greater than might be expected from the cranial length." The value for length of hind foot is also suspect because it is so much smaller than the ranges in the population samples tabulated in table 16. Paula Jenkins, of the Natural History Museum, London, measured the skull for us; the value for CLPMM is an estimate based upon alveolar length.

[c]External measurements for *P. weberi* are from Jentink's (1890:116) description. The value for ear length includes the tuft ("Ear with pencil," as listed by Jentink). Chris Smeenk, at RMNH, measured the skull and dentition of *weber* as well as *leucomus*.

[d]Clara Stefen, at SNSD, measured the skull and dentition of the holotype of *occidentalis*.

18 September. From there, he travelled further west along the coast as far as Paguat, and returned in Gorontalo on 14 November. He arrived back at Kema on 28 November and worked again in Minahasa district, until he finally left Celebes on 14 April 1842 (Veth, 1875; 98, 107; Van Steenis-Kruseman, 1950: 179; and Forsten's unpublished diary).

RMNH 13343 [the lectotype] must be the animal collected on 6 April 1840 near Manado. In Forsten's Celebes diary, a copy of which (written in an unknown hand) is preserved in the archives of the Leiden Museum, the entry for that day relates that his hunter brought "Eene Securus [lapsus by the copyist for Sciurus] welke ik geloof nieuw te zijn, kenbaar aan eene witte plek op de schouderen, ..." (a Sciurus which I believe to be new, characterized by a white spot on the shoulders). In the same diary, Forsten records having collected "eene

TABLE 14
Age, Sex, and External, Cranial and Dental Measurements (mm) for Holotypes of *Prosciurillus alstoni* (includes *sarasinorum*, *mowewensis*, and *elbertae*) and *Prosciurillus rosenbergii* (includes *tingahi*)
The taxa were originally described as members of *Sciurus*.

Variable	*Sciurus sarasinorum* SNSD B3826[a]	*Sciurus mowewensis* NMB 4243[b]	*Sciurus elbertae* SMF 721[c]	*Sciurus rosenbergii* RMNH 13362[d]	*Sciurus tingahi* SNSD B2842[a]	*Sciurus alstoni* ZSI 9546[e]
Type	lectotype	lectotype	holotype	lectotype	lectotype	holotype
Age	adult	adult	adult	young adult	adult	adult
Sex	?	female	?	female	male	?
LHB	—	187	—	—	—	182
LT	—	130	—	—	—	165
LHF	—	41 [43]	—	—	—	—
LE	—	15	—	—	—	—
ONL	42.3	42.2	—	—	—	—
CBL	38.2	40.0	—	—	—	—
ZB	27.2	26.6	—	—	26.1	24.9
IB	17.1	17.0	12.8	16.2	16.6	14.9
LN	12.0	12.5	10.2	13.0	14.4	13.2
LR	19.5	20.5	15.7	19.3	19.6	14.7
BR	7.8	7.7	9.6	9.6	8.3	—
MB	19.6	19.6	—	—	—	—
HBC	15.3	15.1	—	—	—	—
LO	10.1	9.9	—	8.2	11.3	—
LD	9.3	8.8	7.6	8.7	9.1	9.5
LBP	12.0	11.9	10.9	13.2	—	—
PPL	15.9	16.9	—	—	—	—
BBP	9.2	10.4	8.6	9.3	10.3	—
LB	7.5	8.0	—	—	—	—
CLPMM	6.8	7.6	7.3	7.9	7.5	8.0

[a]Clara Stefen, at SNSD, measured the skulls and dentitions of the lectotypes representing *sarasinorum* and *tingahi*.

[b]Values for lengths of head and body, tail, hind foot, and ear are from Roux's (1910: 518) description. These values are approximate because he measured total length, head length, body length, tail with tuft, and tuft, and we don't know his endpoints. His value for hind foot length is without claws; adding 3 mm for claws produces the figure in brackets. Roux's value for length of ear included the tuft and so is not comparable to Musser's values derived from the notch-to-crown dimension. Loïc Costeur, at NMB, measured the skull and dentition, and provided us with a color image of the skin.

[c]Skull and dentition for the holotype of *elbertae* were measured by Gerhard Storch at the Senckenberg Museum.

[d]Chris Smeenk, at RMNH, measured the skull and dentition of *rosenbergii*. Jentink (1879: 38) listed values for lengths of head and body, tail, hind foot, and ear for *rosenbergii* (see table 15), but we don't know which of the 12 syntypes the values came from.

[e]Converted from inches, the unit Anderson (1879) used, to millimeters (see account of *P. alstoni*).

Sciurus" at Pagowat (Paguat) during the week of 5–12 November 1841. This is almost certainly Jentink's skin *k* (RMNH 39394), the pedestal of which reads "Sciurus leucomus Forst Pagowat Célebes" in C.J. Temminck's handwriting, though Forsten is not mentioned as the collector. Jentink (1888) must have overlooked Forsten's diary note and so did not mention this specimen as a type; it is included in the type series here.

EMENDED DIAGNOSIS: *Prosciurillus leucomus* is the first named of the five species in the *P. leucomus* group, sharing with those other members moderate body size and tail equal to, or shorter than, length of the head and body. It contrasts with the other four species by the following combination of pelage traits: **(1)** dorsomedial surface of each ear covered with long black hairs that project beyond the ear rim to form a prominent tuft; **(2)** inside of ears densely covered with bright ochraceous fur; **(3)** white, whitish buff, or grayish white patches of variable intensity and size on the nape behind the ears; **(4)** no

black middorsal stripe extending from neck to base of tail; **(5)** reddish orange, orange-red, or ochraceous underparts; and **(6)** a geographic distribution restricted to the northern peninsula of Sulawesi where it ranges from coastal lowlands to montane forests.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: Apart from the sample collected on Pulau Lembeh off the coast of the northeastern peninsula, all voucher specimens identified as *Prosciurillus leucomus* come from the mainland of the northern peninsula of Sulawesi (see gazetteer and map in fig. 11). Collection localities are scattered over the peninsula from the coastal plain near sea level at the northeastern tip (Likupang and Teteamoet, localities 1 and 2 on the map in fig. 11) to Bumbarujaba (locality 25) near the southern margin of the peninsula. Most localities lie between the coastal plain and 1000 m in what still is or once was tropical lowland evergreen rainforest habitats. The site at 1700 m in montane forest on Gunung Ile-Ile locality is the exception and the highest elevation recorded for any sample of the species.

Bumbarujaba is the most southern collection site for *P. leucomus* and how much farther south it may occur is unknown at present. Approximately 70 km south of Bumbarujaba in the mountains around Danau Lindu where Musser worked are the northernmost records for *P. topapuensis*; and Kuala Navusu, northeast of Lindu on the eastern coastal lowlands of the central core, approximately 100 km south of Bumbarujaba, is the most northern collection site for *P. alstoni* (see gazetteers and map in fig. 11). What kind of squirrel occurs in the landscapes between those two places and the southern end of the northern peninsula is unknown.

In addition to *Prosciurillus leucomus*, several other Sulawesi endemic mammals are recorded from Pulau Lembeh. There is another squirrel, *P. murinus* (see that account); a murid rodent, *Rattus hoffmanni* (Musser and Holden, 1991); a macaque, *Macaca nigra* (Fooden, 1969); the Celebes wild boar, *Sus celebensis* (Groves, 1981); and the babirusa, *Babyrousa babyrousa* (Groves, 1980a; Grubb, 2005: 637, recognizes several species, listing the sample from Pulau Lembeh as *B. celebensis*). The closest points between island and mainland are less than a kilometer apart, and the Lembeh Strait is shallow, less than 50 m deep (Sheet NA 51-12). During periods of Pleistocene glaciation when sea level in the Indomalayan region dropped by at least 120 m (Bintanja et al., 2005) and possibly 200 m (Morley and Flenley, 1987), Lembeh would have been part of the mainland (see the map in Fooden, 1969: 65). With post-glaciation rise in sea level, rodent and other mammal populations on Lembeh were separated from the mainland. This scenario seems the most likely explanation for the occurrence of the three rodent species on the island, although we cannot rule out over-water dispersal. Whatever the process, squirrels in available samples of each species (as well as the other mammals referred to above) are similar in pelage coloration and morphometric traits to those in samples from the mainland, suggesting no significant genetic isolation between island and mainland populations.

DESCRIPTION: Müller and Schlegel (1844: 87) aptly described the diagnostic features of *Prosciurillus leucomus* (translated from the original Dutch by Chris Smeenk, in litt., 2008; the Dutch text is reproduced in appendix 2):

> 9.) **Sciurus leucomus**, Forsten, n. sp. Size and shape as in the two preceding ones [*Sciurus vittatus*, a synonym of the Sundaic *Callosciurus notatus*, and *Sciurus nigrovittatus*, currently *Callosciurus nigrovittatus*; see Corbet and Hill, 1992; 291–292]. Inside of the ears densely covered with brownish yellow [hairs], back [of the ears] with long black hairs, protruding far above the ears. Colour of the upper parts and outside of the legs olive-brown; the hairs with rusty-yellow rings and partly black tips. Tail checkered with the three colours mentioned. A large white patch behind the ears, on either side of the neck. Lower parts of the body rusty coloured, tending to reddish-brown. Celebes.

Samples from the northern peninsula of Sulawesi portray a squirrel of modest body size with a tail averaging as long as, or only slightly shorter than, length of head and body (length of head and body, 165–188 mm; length of hind foot, 43–47 mm; see table 15). The dense, uniformly thick (12–15 mm) coat

TABLE 15

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g), Derived from Samples of *Prosciurillus leucomus*, *Prosciurillus alstoni*, *Prosciurillus weberi*, and *Prosciurillus rosenbergii*[a]

Mean ± 1 SD, observed range (in parentheses), and size of sample are listed. Mean values were used to compute LT/LHB. Specimens measured are listed below.[b]

Variable	*P. leucomus* northeastern peninsula (Likupang, Teteamoet, Temboan)	*P. leucomus* northern peninsula (Sungai Paleleh, Tolitoli, Labuan Sore)	*P. alstoni* central core (Pinedapa)	*P.alstoni* central core (Kuala Navusu, Sungai Tolewonu)	*P. weberi* central core (Masamba)	*P. rosenbergii* Kepulauan Sangihe
HB	174.5 ± 5.46 (165–188) 18	174.3 ± 5.96 (165–180) 7	167.0 ± 4.46 (160–175) 20	176.9 ± 8.36 (157–195) 40	187, 156	190
LT	165.9 ± 13.83 (140–190) 17	171.3 ± 10.36 (150–181) 7	165.5 ± 7.94 (150–180) 18	156.5 ± 8.47 (135–175) 35	142, 164	180
LT/LHB (%)	95	98	99	89	76, 95	95
LHF	44.5 ± 1.15 (43–47) 18	44.3 ± 0.95 (43–45) 7	42.5 ± 1.36 (40–45) 20	45.1 ± 1.38 (43–48) 40	43, 42	42
LE	—	—	—	17.1 ± 0.91 (15–19) 40	17, 21	17.5
WT	—	—	—	176.9 ± 18.38 (135–210) 40	—	

[a]Specimens from the northern and northeastern peninsulae, along with Pinedapa in the central core were measured by H.C. Raven in the field. He did not measure ear lengths or obtain weights. Musser remeasured the dry hind foot of all of Raven's material.

Specimens constituting the samples from Kuala Navusu and Sungai Tolewonu were measured and weighed by Musser in the field (see the methods section).

Values for *P. weberi* come from two specimens. Those on the left are given by Jentink (1890: 116), presumably from the lectotype, but we are not certain (see table 12); the ear measurement is Jentink's "ear with pencil." Values on the right were taken from the skin label of MZB 6253. Most other examples of the species are without measurements on the skin tags; the exception is a specimen for which the values are unreliable. We cannot vouch for the accuracy of the measurements for *P. weberi* listed here and include them only to provide an estimate of body size, which is not so different from the other members of the *P. leucomus* group.

Values for *P. rosenbergii* are from a specimen measured by Jentink (1879: 38).

[b]Likupang: USNM 216786–88, 216791. Teteamoet: USNM 216769, 216772–79, 216784, 216785. Temboan: USNM 217825. Sungai Paleleh: USNM 200270–72. Tolitoli: USNM 200274. Labuan Sore: USNM 218074–76. Pinedapa: USNM 219511, 219512, 219515–17, 219521, 219523, 219525, 219527–29, 219531–33, 219535–40. Kuala Navusu: AMNH 226076–090, 226092–101. Sungai Tolewonu: AMNH 226511–25.

covering upperparts of head and body is dark brown flecked with black and orange along the midline of the body from forehead to base of tail, but grading into brownish gray spotted with black and pale buff along sides of the body, forelegs, and hind legs. Dorsal surfaces of the front and hind feet resemble the head and back in most specimens; some are slightly darker or buffy gray. Coloration of the body fur results from the interplay of dark gray curly underfur; longer overfur composed of black hairs, each interrupted by a subterminal orange or pale buffy band; and black guard hairs barely projecting beyond the overhair layer.

This dorsal background is interrupted by distinctive color patterning on the head, ears, and neck. Top and sides of the muzzle are ochraceous, and the cheeks are either the same color as the top of the head or a grayish buff that extends to each nape patch. A prominent, dense black tuft covers the medial surface of each ear, projecting 5–10 mm beyond the free dorsal rim of the ear. Behind each ear on the nape is a large and conspicuous white, whitish buff, or whitish

TABLE 16

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g), Derived from Samples of *Prosciurillus topapuensis* from the West-Central Core of Sulawesi[a]

Mean ± 1 SD, observed range (in parentheses), and size of sample are listed. Mean values were used to compute LT/LHB. Specimens measured are listed below.[b]

Variable	Sungai Miu, Sungai Sadaunta	Gunung Kanino, Gunung Nokilalaki	Gunung Lehio	Besoa, Lindu trail	Rano Rano	Pegunungan Latimojong
HB	179.6 ± 6.47 (170–190) 11	172.8 ± 6.41 (167–190) 12	160.6 ± 3.68 (155–168) 9	163.4 ± 8.68 (155–175) 5	162.4 ± 4.96 (155–170) 14	162.3 ± 6.52 (151–169) 10
LT	163.8 ± 7.07 (155–175) 10	141.1 ± 11.94 (120–150) 7	153.7 ± 10.72 (140–175) 9	147.4 ± 10.43 (135–162) 5	143.9 ± 12.30 (120–160) 14	136.0 ± 4.21 (130–145) 9
LT/LHB (%)	91	82	96	90	89	84
LHF	47.6 ± 0.93 (47–50) 11	44.8 ± 1.53 (43–49) 12	42.1 ± 1.27 (40–44) 9	41.4 ± 0.89 (40–42) 5	41.6 ± 0.94 (40–43) 14	40.3 ± 1.16 (38–42) 10
LE	19,7 ± 0.79 (18–21) 11	19.3 ± 1.55 (15–21) 12	—	—	—	—
WT	184.6 ± 18.09 (150–210) 11	160.0 ± 15.08 (130–180) 12	—	—	—	—

[a]Specimens from Gunung Lehio, Besoa and Lindu trail, and Rano Rano were measured by H.C. Raven in the field. He did not measure ear lengths or obtain weights. Musser remeasured the dry hind foot of all of Raven's material. Specimens constituting the samples in the first two columns were measured and weighed by Musser in the field (see Methods). Squirrels from Pegunungan Latimojong were measured by G. Heinrich in the field. He did not obtain weights. Heinrich measured ear length from base to crown, which results in a smaller value than notch to crown; we have omitted his values because they are not comparable to Musser's values, which measured notch to crown. Musser remeasured the dry hind feet of Heinrich's material.

[b]Sungai Miu: AMNH 224042. Sungai Sadaunta: AMNH 224041, 224581–88, 226835. Gunung Kanino: AMNH 223532–35, 225501–507. Gunung Lehio: USNM 218714–18, 218720–23. Besoa: USNM 219485, 219488, 219489, 219502. Lindu Trail: USNM 218719. Rano Rano: USNM 219484, 219486, 219487, 219490–96, 219498, 219499, 219501, 219503. Pegunungan Latimojong: AMNH 196535–41, 196544–46.

gray patch (20–30 mm long, 15–20 mm wide), its shape resembling an epaulet (pointed toward the posterior margin); and the inner surface of each pinnae is densely clothed with bright ochraceous hairs. The overall visual pattern evolves around an ear with an ochraceous center rimmed by black that is set off against a large whitish postauricular epaulet (see the color plate in fig. 9). While the black tufting is present in all geographic samples of *P. leucomus*, the nape patches vary in size, color, and frequency of occurrence; these aspects are addressed in the sections covering geographic variation and synonyms.

The short (5–7 mm thick) ventral coat ranges from bright reddish orange through orange-red to ochraceous; orange-red predominates in the samples. The hairs forming the ventral covering are pale gray along their basal half and deeply pigmented along the distal half.

The tail, equal to or slightly shorter than length of head and body (LT/LHB = 95%–98%, see table 15), is covered in long hairs, each patterned by alternating black and buffy or orange bands. The overall effect is rings of black and buff with buffy bands outlining margins of the tail and long black hairs forming a black terminal tuft.

Females have six teats, positioned as one postaxillary pair and two inguinal pairs. Litter size has not been recorded for *P. leucomus*, but one young would be usual if this aspect of reproduction is like its allopatric relatives, *P. topapuensis* and *P. alstoni* (table 57).

The skull of *P. leucomus* closely resembles those of *P. alstoni* and *P. topapuensis*, which are illustrated in figures 12–14. Evident in those drawings is the convex dorsal curve of the skull reflecting pronounced cranial flexion, short and wide nasals and rostrum, wide

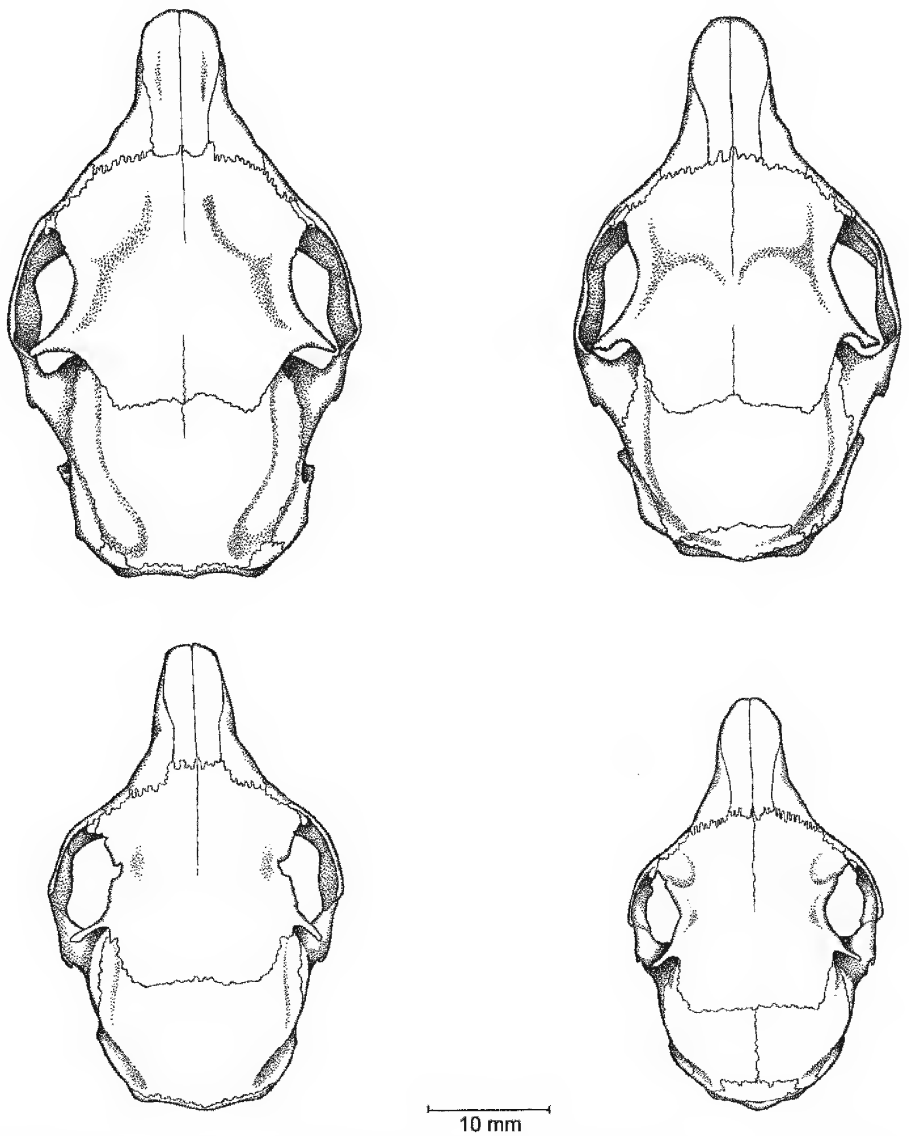

Fig. 12. Dorsal views of skulls representing species of *Prosciurillus*. Top row, left to right: *P. alstoni* (AMNH 226076; Kuala Navusu; ONL = 46.6 mm) and *P. topapuensis* (AMNH 225504; Gunung Kanino; ONL = 45.0 mm); we employ these two as exemplars of species in the *P. leucomus* group. Bottom row, left to right: *P. abstrusus* (AMNH 101378, holotype; Pegunungan Mekongga; ONL = 38.2 mm) and *P. murinus* (AMNH 225496; Gunung Kanino; ONL = 34.4 mm); these are the only species comprising the *P. murinus* group.

interorbital region, postorbital processes that are even with the anterior curve of braincase, faint and widely spaced temporal ridges that do not coalesce into a sagittal crest, posterior margin of the bony palate situated slightly anterior to backs of the parallel tooth rows, wide pterygoid fossae (each triangular as seen from ventral view), conspicuous posterior maxillary notch in the bony palate between the end of the tooth row and anterior portion of the pterygoid fossa, proodont (procumbent) upper incisors, and small third molar compared with the larger second and third molars and fourth premolar. The dentary has a short coronoid process and deep ramus, and deeply concave (even angularly concave

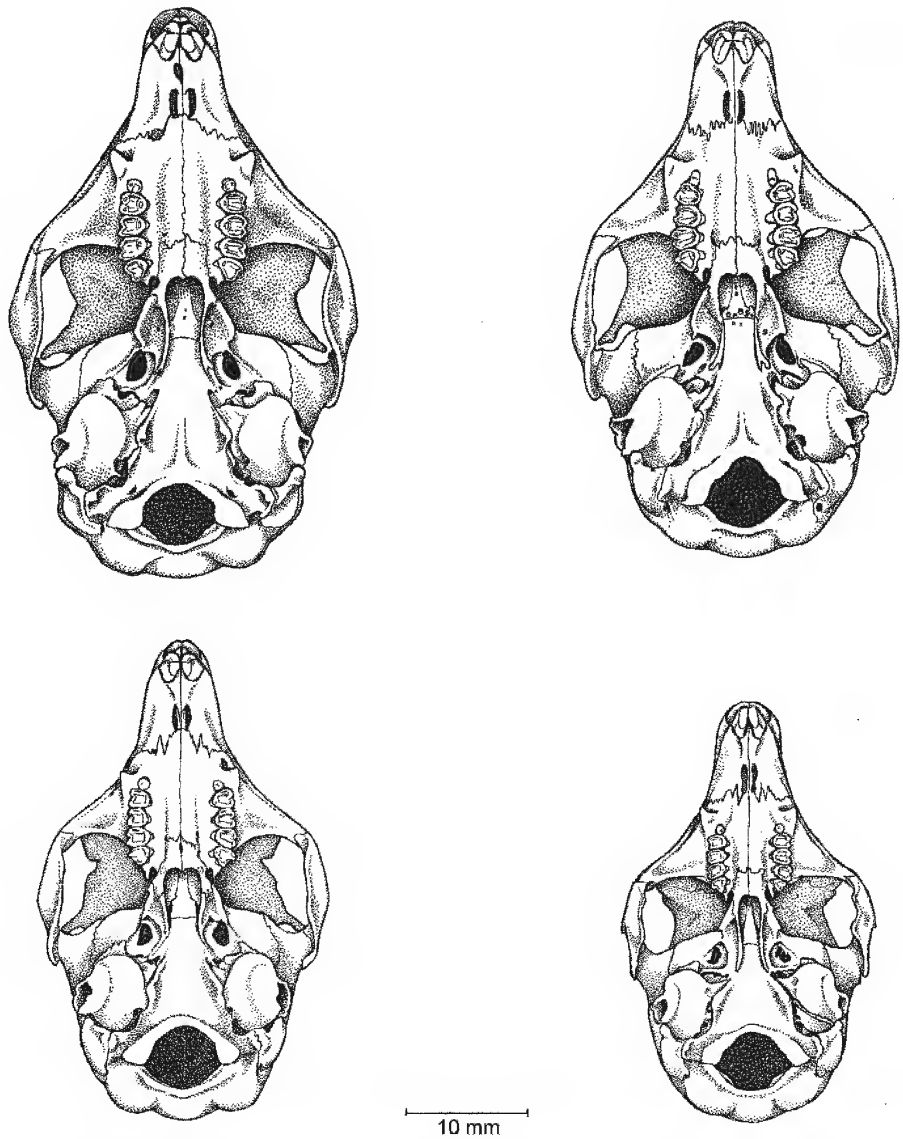

Fig. 13. Ventral views of the skulls portrayed in figure 12. *Prosciurillus alstoni* and *P. topapuensis* are on top, *P. abstrusus* and *P. murinus* on the bottom.

in some specimens) posterior margin between condyloid and angular processes. Cranial and dental measurements are summarized in tables 17 and 19.

COMPARISONS: The geographic distribution of *P. leucomus* is allopatric to the ranges of *P. topapuensis* and *P. alstoni* to the south in the central core of Sulawesi, and comparisons between *P. leucomus* and each of these two species will be presented in those accounts. No other samples of squirrels from regions on Sulawesi outside of the northern peninsula show the distinctive color patterns seen in *P. leucomus* (see the diagnostic traits compared in table 12).

Other than a close resemblance in body size, tail proportions, and some cranial dimensions, *P. leucomus* is also unlike *P. rosenbergii*, the only species occurring in the Sangihe Archipelago north of the northeastern tip of Sulawesi, and north of the distribution of *P. leucomus*. It is the the only

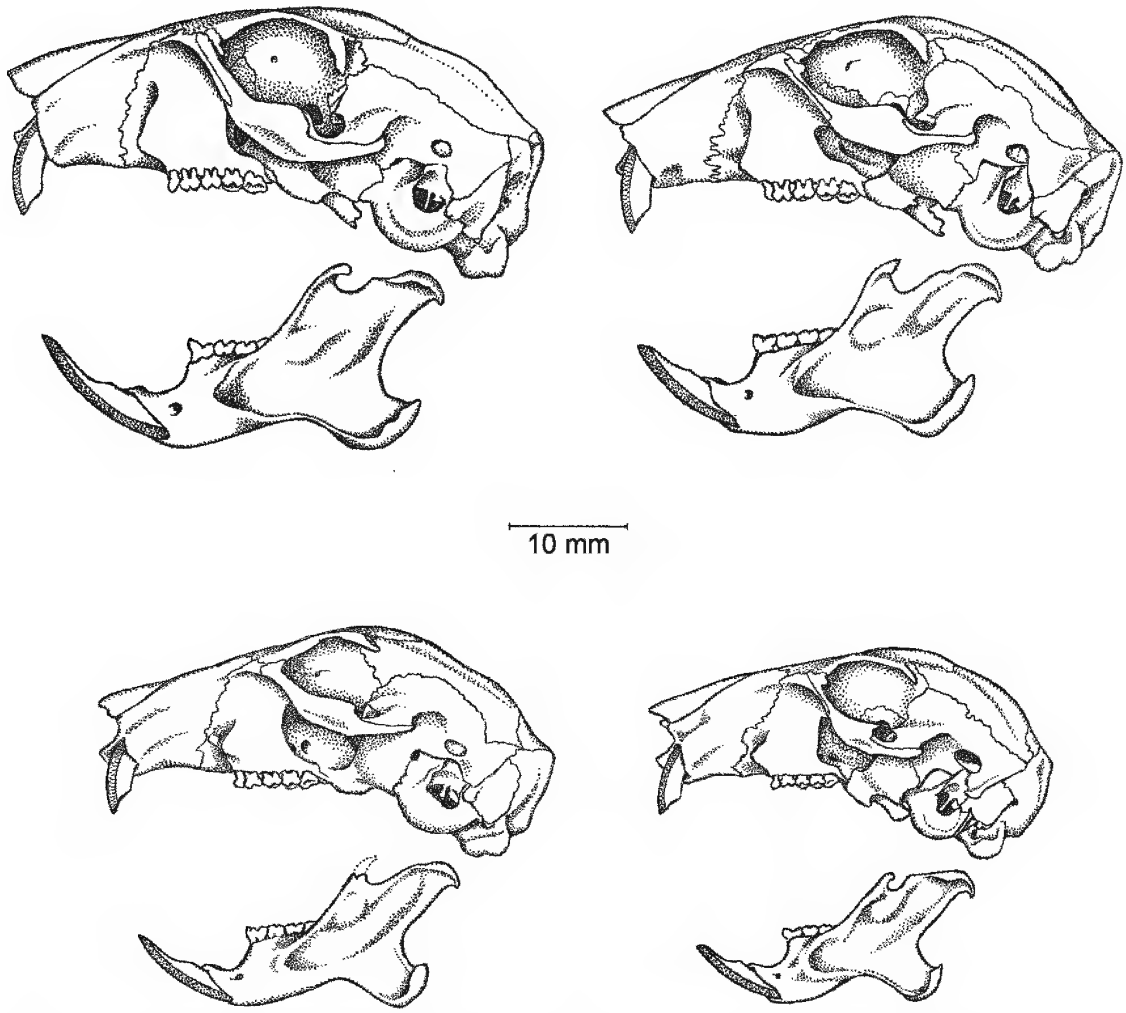

Fig. 14. Side views of the skulls, along with mandibles, exhibited in figures 12 and 13. Top row, left to right: *Prosciurillus alstoni* and *P. topapuensis*. Bottom row, left to right: *P. abstrusus* and *P. murinus*.

member of the *P. leucomus* group with uniform dark chestnut upperparts and brownish gray or buff underparts. No ear tufts, nape patches, or middorsal black stripe mark the dorsal coat (table 12). Unfortunately, we do not have intact skulls from the samples of *P. rosenbergii* and cannot provide cranial and dental morphometric comparisons between it and *P. leucomus*.

GEOGRAPHIC VARIATION: Samples from throughout the geographic range of *P. leucomus* (the northern peninsula of Sulawesi) contain squirrels closely similar in body size (table 15). The noticeable geographic variation concerns coloration of the muzzle and the underparts, along with changes in color and extent of the nape patches. Most specimens from about the middle of the northern peninsula—in the region of Gorontalo (00°31′N, 123°03′E)—to the east have ochraceous muzzles and cheeks, prominent black ear tufts, large white or whitish buff nape patches, and reddish orange underparts. Squirrels in samples from west of Gorontalo show pale buff or gray muzzles and cheeks (as opposed to bright ochraceous), and exhibit considerable variation in extent and color of the nape patches. These patches may

TABLE 17

Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Combined Population Samples of Species in the *Prosciurillus leucomus* Group

Mean ± 1 SD and observed range (in parentheses) are listed; size of sample follows the parentheses for *P. rosenbergii*.

Variable	*P. leucomus* $N = 26$	*P. alstoni* $N = 63$	*P. weberi* $N = 5$	*P. topapuensis* $N = 50$	*P. rosenbergii*[a]
ONL	45.7 ± 0.33	44.4 ± 0.96	44.2 ± 1.06	44.5 ± 1.35	—
	(44.1–47.6)	(40.7–46.5)	(42.7–46.7)	(42.0–47.2)	
CBL	41.2 ± 1.01	39.8 ± 0.92	38.8 ± 0.99	39.9 ± 1.45	—
	(39.6–43.8)	(37.8–43.3)	(37.4–40.1)	(37.2–43.0)	
ZB	27.9 ± 0.75	27.3 ± 0.82	25.4 ± 1.10	26.4 ± 0.79	25.8 ± 0.42
	(26.8–29.5)	(25.4–29.1)	(24.2–27.0)	(24.4–28.1)	(25.5–26.1) 2
IB	17.6 ± 0.55	17.1 ± 0.70	15.5 ± 0.74	15.9 ± 0.65	15.6 ± 1.08
	(16.7–18.8)	(15.2–19.1)	(14.4–16.5)	(14.4–17.2)	(13.7–16.6) 6
LN	11.7 ± 0.60	12.3 ± 0.54	11.7 ± 0.64	12.7 ± 0.61	13.1 ± 0.75
	(11.7–14.0)	(11.2–13.9)	(10.9–12.5)	(11.5–14.3)	(12.5–14.4) 5
LR	20.5 ± 0.79	19.7 ± 0.63	18.9 ± 0.92	19.5 ± 0.84	19.0 ± 0.46
	(19.2–22.2)	(18.3–21.3)	(18.1–20.4)	(18.8–21.3)	(18.4–19.6) 5
BR	8.6 ± 0.60	8.4 ± 0.51	9.3 ± 0.51	8.6 ± 0.55	9.6
	(7.3–9.9)	(7.6–9.6)	(8.6–9.8)	(7.3–9.7)	
MB	19.3 ± 0.41	19.3 ± 0.45	18.8 ± 0.51	18.5 ± 0.63	—
	(18.4–20.1)	(18.3–20.5)	(18.0–19.3)	(17.2–20.0)	
HBC	15.1 ± 0.47	15.0 ± 0.42	14.6 ± 0.47	15.2 ± 0.44	—
	(14.0–16.3)	(14.2–15.8)	(14.1–15.2)	(14.3–16.1)	
LO	10.5 ± 0.32	10.2 ± 0.32	10.0 ± 0.40	9.6 ± 0.40	10.2 ± 1.17
	(9.7–11.0)	(9.3–11.0)	(9.5–10.5)	(8.8–10.3)	(8.2–11.3) 5
LD	9.0 ± 0.43	8.9 ± 0.43	9.3 ± 0.52	8.9 ± 0.54	8.9 ± 0.46
	(8.1–10.0)	(8.0–10.1)	(8.8–10.1)	(8.0–10.1)	(8.7–9.4) 6
LBP	12.5 ± 0.49	12.5 ± 0.38	12.0 ± 0.66	12.2 ± 0.56	12.4 ± 0.76
	(11.5–13.5)	(11.7–13.5)	(11.2–12.9)	(11.1–13.6)	(11.7–13.2) 3
PPL	17.6 ± 0.40	17.2 ± 0.66	17.8 ± 0.64	16.9 ± 0.75	—
	(16.7–18.4)	(15.4–19.1)	(16.9–18.4)	(15.6–18.8)	
BBP	10.0 ± 0.29	9.5 ± 0.34	9.4 ± 0.59	9.6 ± 0.37	10.1 ± 0.45
	(9.4–10.5)	(8.6–10.4)	(8.6–10.0)	(8.8–10.4)	(9.3–10.5) 6
LB	8.0 ± 0.23	8.0 ± 0.28	7.6 ± 0.19	7.6 ± 0.35	—
	(7.7–8.7)	(7.2–8.6)	(7.3–8.0)	(7.0–8.5)	
CLPMM	7.7 ± 0.24	7.2 ± 0.22	6.8 ± 0.27	7.4 ± 0.29	7.6 ± 0.25
	(7.1–8.0)	(7.3–8.4)	(6.5–7.2)	(6.8–8.0)	(7.3–7.9) 6

[a]Values entered here are from the lectotype of *rosenbergii* (measured by Chris Smeenk) and lectotype and four paralectotypes of *tingahi* (measured by Clara Stefen); see table 14. All these skulls are damaged, as are the additional specimens that were measured by Feiler (1990: 91). Measurements for *P. rosenbergii* were not employed in any multivariate analyses.

be prominent and white or whitish buff as in the squirrels inhabiting the peninsula east of the Gorontalo region; diluted, consisting of diffuse grayish patchs barely distinguishable from the rest of the neck (a few individuals from east of Gorontalo have diluted nape patches); or not present, the areas behind the ears being the same color as the rest of the neck and upperparts of the head and body. All these specimens retain a prominent black tuft projecting beyond the rim of each ear. Underparts of specimens in the western samples are paler: ochraceous is the dominant hue, a very few specimens exhibit reddish orange venters; reddish orange characterizes most specimens from east of Gorontalo, but some individuals show orange-red or ochraceous underparts. The variation in color of the nape patches and their extent has been the stimuli for recognizing the

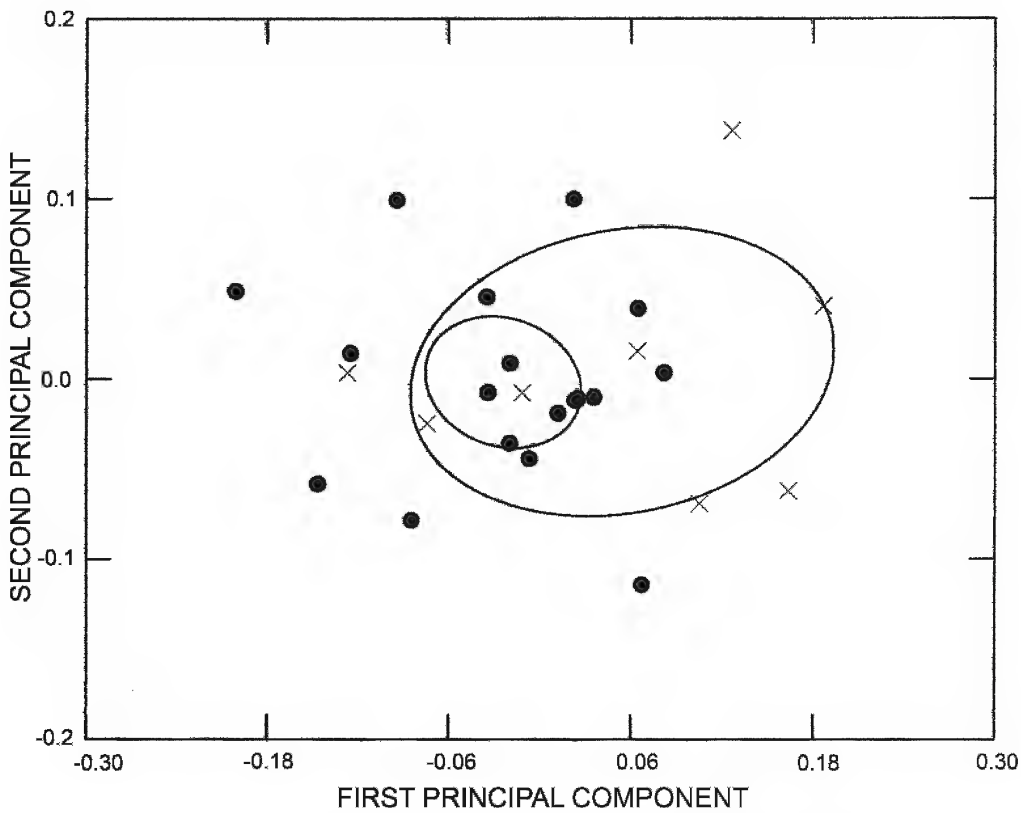

Fig. 15. Specimen scores representing two population samples of *Prosciurillus leucomus* projected onto the first and second principal components extracted from principal-components analysis. Symbols identifying samples are: filled circle = northeastern peninsula (Likupang, Teteamoet, Rurukan, Temboan; $N = 18$); × = western segment of northern peninsula (Bumbulan, Sungai Paleleh, Gunung Ile-Ile, Labuan Sore, Bumbarujaba; $N = 8$). Ellipses outline 95% confidence limits for the specimen scores representing each population sample. See table 18 for correlations and percent variance.

western peninsular samples as *P. leucomus occidentalis* (Meyer, 1898: 2). We elaborate on this variation and its significance in the section discussing synonyms.

The magnitudes of cranial and dental dimensions measured in our samples are similar (table 19). Mean values for certain dimensions average greater in the western samples than those from the northeastern end of the peninsula but the differences are not significant, as is reflected in figure 15 where specimen scores representing two population samples of *P. leucomus*—one from the northeast, the other from the western portion of the peninsula (identified in table 1)—are projected onto the first and second principal components extracted from principal-components analysis. The spread of scores along the first axis is primarily influenced by size, the larger (and sometimes older) adults spreading to the right, the smaller (and usually, but not always, younger) adults to the left. Covariation in most cranial variables spread the scores along the first axis with the most influential being breadths of the interorbit and rostrum, and lengths of the nasals, rostrum, diastema, and bony palate (table 18). The western squirrels have, on average, a larger facial skeleton, but the contrast is not significant as reflected in the complete overlap of the ellipses outlining the 95% confidence limits for the specimen scores representing each population sample.

The geographic variation in expression of nape patches within *P. leucomus* does not appear to have a counterpart in cranial and dental morphometric variation among our samples. However, other than the large series

TABLE 18
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus leucomus* from the Northern Peninsula
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 15.

Variable	PC1	PC2
ONL	0.013	0.002
CBL	0.018	0.009
ZB	0.016	0.009
IB	0.021	0.005
LN	0.024	−0.029
LR	0.031	−0.006
BR	0.061	−0.019
MB	0.008	0.014
HBC	−0.000	0.021
LO	0.005	0.010
LD	0.040	0.019
LBP	0.026	0.022
PPL	0.013	0.001
BBP	0.011	0.013
LB	−0.004	0.010
CLPMM	−0.004	−0.003
Eigenvalues	0.009	0.003
Percent variance	44.988	16.247

from Bumbulan, we have small numbers of squirrels from elsewhere in the western part of the peninsula, especially from that arc between Bumbulan and Labuan Sore at the base of the peninsula. Large samples are currently available from both west (Bumbulan, for example) and east (the Minahasa region) of Gorontalo, but we were still hampered in our investigation of cranial and dental morphometric variation because so many of the skulls are damaged, the result of sampling by shotgun. Clearly, the results we describe here will have to be tested by analyzing samples from regions now unrepresented by collections, and larger series of specimens containing intact skulls.

Morphology of available samples of sucking lice (*Hoplopleura*) varies slightly in accordance with host populations of *P. leucomus* but the samples of parasite and host are small. A few female and nymphal lice were found on a squirrel from Rurukan (*leucomus* morphology), east of the Gorontalo region, and on one collected at Labuan Sore (*occidentalis* morphology), to the west of Gorontalo at the base of the northern peninsula. Specimens in each sample of *Hoplopleura* differ slightly in shapes of the paratergal plates and lengths of their apical setae. However, males of these lice were not available for study (morphology of male genitalia is often the most important distinguishing character for different species of lice) and we consider the variation in the female paratergal plates to lie within the limits of a single species, *Hoplopleura leucomus*, n. sp. (see accounts describing the lice).

The variation in pelage traits among samples of squirrels collected over the northern peninsula roughly coincides with peninsular distributions of murid rodents and monkeys. *Macaca hecki* occurs from the base of the northern peninsula to the Gorontalo region, which coincides with the distribution of the color pattern variation in *P. leucomus* that has been recognized as *occidentalis*. *Macaca nigrescens* and *M. nigra* have allopatric ranges east of the Gorontalo area and extending to the northeastern tip and onto the offshore islands Pulau Lembeh and Pulah Talise (Fooden, 1969; Groves, 1980b, 2005); combined ranges of these two macaques are congruent with that of the typical form of *Prosciurillus leucomus*, which occurs east of the Gorontalo region all the way to the northeast tip of the peninsula and on Pulau Lembeh. The murids, *Echiothrix leucurus*, *Bunomys fratrorum*, *Taeromys taerae*, and *Rattus xanthurus* are also known only from this eastern segment of the peninsula (from Gorontalo eastward); their phylogenetic counterparts (*Echiothrix centrosa*; *Bunomys andrewsi*, *B. penitus*, and *B.* sp.; *Taeromys hamatus*; and *Rattus marmosurus*) range to the west of Gorontalo into Sulawesi's central core, or have been recorded only from the central core and the southeastern and southwestern peninsulae (Musser, MS; Musser and Carleton, 2005).

ECOLOGY: We lack first-hand experience with *P. leucomus* in the wild and are unaware of any published observations. Judged from its close resemblance in body size and tail proportions to populations of squirrels from the central core of Sulawesi (*P. topapuensis* and *P. alstoni*) that Musser encountered, we suspect that *P. leucomus* is an habitué of the canopy, descending to the ground between gaps in the canopy and likely for some

foraging. Soft fruits and insects probably comprise the diet.

ECTOPARASITES: The host-specific sucking louse *Hoplopleura leucomus*, n. sp. (described in a following section), is the only ectoparasite recorded from *Prosciurillus leucomus* (table 56).

SYMPATRY: The range of *P. leucomus* on mainland Sulawesi overlaps those of *P. murinus*, *Rubrisciurus rubriventer*, and the ground squirrel *Hyosciurus ileile* (table 6). Both *P. leucomus* and *P. murinus* have been collected on Pulau Lembeh off the northeastern coast of the northern peninsula (table 4).

SYNONYMS: Only one synonym is attached to *Prosciurillus leucomus*, which we discuss below.

Sciurus leucomus occidentalis Meyer, 1898: 2. LECTOTYPE: SNSD B168 (stuffed museum study skin and a skull; see table 13 for measurements), an adult female collected by Riedel in 1875. TYPE LOCALITY: Gorontalo, 00°31′N, 123°03′E, near sea level on the southern coastal plain of the northern peninsula, Propinsi Sulawesi Utara, Indonesia (locality 15 in gazetteer and map in figure 11).

To understand why we regard SNSD B168 to be the lectotype and Gorontalo to be the type locality, we must begin with Meyer's (1896) monograph covering the mammals of Sulawesi where he provided (pp. 25–26) an account of "*Sciurus leucomus*" and described the variation in expression of the white patch on the nape just behind each ear (see appendix 8 where the account is reproduced in the original German). Meyer set the context by noting Anderson's (1879: 252) observations derived from his visits to the museums in Paris and Leiden where he had examined specimens of "*Sciurus leucomus*." According to Anderson,

> The series in the Leyden and Paris Museums from the Celebes prove that the white on the side of the neck is not always present, for one specimen shows it disappearing and in another there is no trace of it, and others lead from the one to the other extreme, but when this neck spot is full developed it forms a great violet-white lappet.

Meyer studied 16 specimens from the Minahasa region (collected at Main, Manado, Lotta, and Amurang; see our gazetteer), two from Pulau Lembeh (locality 3 in our gazetteer), and two collected at Gorontalo (locality 15 in our gazetteer), on the northern peninsula far to the west of the Minahasa region. In his specimens at hand from the Minahasa district of the northeastern peninsula, the nape patches were expansive and white (white mixed with a few black-tipped or buffy-tipped hairs in some of our specimens), vividly contrasting with the large black ear tufts and brown dorsal fur, a pattern characteristic of *leucomus* from the northeast. The two specimens from Gorontalo, however, exhibited a different pattern. Both were adults as judged by characteristics of the skull and both had prominent black ear tufts, but one (B168) completely lacked the nape patches, and the other (857) exhibited only traces of the pattern: "Auf der anderen Seite zeigt von den 2 Exemplaren von Gorontalo das eine (B 168) keine Spur von Weiss, und es ist nach dem Schädel ein ganz altes Individuum, und das andere (857), ebenfalls adult, hat den Fleck nur sehr schwach entwickelt" (Meyer, 1896: 26).

Meyer also referred to material at Leiden that had been collected in the Gorontalo region. Specimens from Panibi, Modelido, and Limbotto (see our gazetteer) resembled the two Dresden specimens from Gorontalo in showing only faint nape patches or completely lacking them. On the other hand, Meyer admitted that examples from Tulabello, just east of Gorontalo, and Paguat, far to the west of Gorontalo, had prominent, whitish nape patches.

We see a similar range in variation in color and size of nape patches among our specimens stored in the USNM and AMNH. In USNM samples from the northwestern and western portions of the northern peninsula (Sungai Paleleh, Tolitoli, Labuan Sore, and Bumbarujaba; see the gazetteer), the black ear tufts are prominent but the nape patches are reduced in size and intensity as compared to those on squirrels from east of Gorontalo. The variation consists of individuals with modest white or whitish buff nape patches behind each ear (USNM 218074 from Labuan Sore, for example); specimens expressing diffuse patches, usually grayish or buffy white, barely distinguishable from the

neck (USNM 218077, another squirrel from Labuan Sore); or a few specimens with no patches—at least the sides of the neck are indistinguishable from the bright brown fur tipped with buff over the head and body (USNM 200271 from Sungai Paleleh).

The variation in two geographic AMNH samples from west of Gorontalo is also illustrative. Twenty specimens come from Bumbulan (see gazetteer). One individual has large white nape patches that match the color and size of the patches characterizing the samples east of Gorontalo. Seven specimens have large, conspicuous nape patches, but they are dull compared with the bright patches seen in the eastern samples—gray or buffy gray instead of white. The patches are inconspicuous on most of the remaining specimens—small buffy areas behind the ears—and three lack the patches.

Sixteen AMNH specimens are from Matinan and Gunung Ile-Ile (see gazetteer), west of Bumbulan. All have prominent black ear tufts, similar in size to those on squirrels from east of Gorontalo. Six have smaller, inconspicuous buffy nape patches that slightly contrast with the rest of the fur covering the neck. Nape patches are conspicuous on squirrels in the remainder of the sample, but the patches are slightly smaller and duller (gray or buffy white) than those characterizing squirrels occurring east of Gorontalo.

In 1898, Meyer, under an account titled "*Sciurus leucomus occidentalis* n. subsp." (p. 2), referred to his earlier report (Meyer, 1896) where he had described the whitish nape patches on the two squirrels from Gorontalo as being weakly developed or not present. In that report he had also speculated that the variation in expression of the nape patch seen on the two Gorontalo specimens might represent an intermediate pattern. At one extreme would be the pattern found in squirrels from the northeastern end of the northern peninsula: large, black ear tufts contrasting with expansive white nape patches. The sample of "*Sciurus tonkeanus*" (Meyer, 1896: 25) from the east-central arm of central Sulawesi, which lacks both black ear tufts and nape patches (ears and neck are the same color as the head and body; see our account of *P. alstoni*) would define the opposite extreme. Large black ear tufts combined with nape patches either reduced in size and intensity or absent would be the intermediate pattern, which is characteristic of squirrels inhabiting the northern peninsula in and west of the Gorontalo area.

Additional specimens collected by Paul and Fritz Sarasin and sent to Meyer for identification supported, in Meyer's view, his supposition. Meyer's identifications of the specimens collected by the Sarasins are recorded in his 1898 publication where he focused on contrasting variation in expression of the nape patches among the specimens. Five (three adult males, one adult female, and one juvenile female) from the Minahasa region (three from Tomohon, one from Kottabuna on the border of Minahasa, and one from "Minahasa") exhibited the prominent white nape patches typical of *leucomus* ("spotted" ["gefleckte Form"] as Meyer described them). Two other squirrels, both males, were collected in the northern peninsula west of Gorontalo and lacked the nape patches ("unspotted" ["ungefleckte Form"]). One of these came from between Kottabongon and Bolang Mongondo at about 250 m, the other from the north side of the Matinan ("Matinang") range at about 1000 m. After some discussion, Meyer (1898: 3) proclaimed that the "unspotted" form could be separated as a subspecies only from typical *leucomus* because of the apparent transition between the two forms: "Die ungefleckte Form lässt sich nur als Subspecies von *leucomus* abtrennen, da Uebergänge zwischen beiden vorhanden zu sein scheinen. ..."

Some researchers who consulted only Meyer's 1898 report where he proposed the taxon *occidentalis* have assumed that Meyer regarded the two "unspotted" specimens collected by the Sarasins to be comparable to cotypes. But, as was the custom at that time, Meyer did not select a type, did not identify types of any kind, and did not designate a type locality. For him (Meyer, 1898: 3), the range of *occidentalis* extended from west of the Minahasa region (which is in the northeastern tip of the northern peninsula, the range of typical *leucomus*) to the Buol area (near Tolitoli; see gazetteer) in the northwest ("westlich von der Minahasa bis Buol"). His view was shaped not only by

the two "unspotted" examples collected by the Sarasins and listed in the later 1898 publication, but also by the specimens he discussed in his earlier 1896 report: the two Dresden specimens from Gorontalo and the Leiden material collected around the Gorontalo region and farther west.

Without consulting both of Meyer's reports, any attempt to identify a type specimen and pinpoint the type locality is frustrating and has yielded different results from researchers. Ellerman (1940: 375), for example, listed *occidentalis* as being simply from "West Celebes." In 1954, Laurie and Hill (p. 93) listed the type locality as "Between Kottabangon and Bolang Mongondo, north-western Celebes," which suggests that the first of the two of the Sarasin's "unspotted" specimens listed by Meyer in 1898 would be the type. This locality designation was followed by Corbet and Hill (1992: 304). Feiler (1999: 407) in his catalog of types housed at Dresden, however, identified the "holotype" of *occidentalis* as SNSD B168, the squirrel mentioned by Meyer (1896) as being from Gorontalo. But Feiler, confusingly, listed the type locality as "Sulawesi, Nordseite der Matinang-Kette, etwa 1000 m hoch," which is the collection locality of the Sarasin's second "unspotted" squirrel listed in Meyer's 1898 publication; Feiler does not record the presence of that specimen in Dresden.

Our attempt to examine all the specimens studied by Meyer has also proved frustrating. Some of the Dresden material Meyer discussed in his 1896 report is no longer in that institution (C. Stefen, in litt., 2008), but the Leiden specimens are still present in the Nationaal Natuurhistorisch Museum (C. Smeenk, in litt., 2008). Three of the five "white-spotted" squirrels collected by the Sarasins from the Minahasa region and identified in Meyer's 1898 publication are in the collection of the Naturhistorisches Museum Basel (L. Costeur, in litt., 2008; see gazetteer), another is in the British Museum (P. Jenkins, in litt., 2008). We also located only one of the Sarasin's two "unspotted" specimens, the example from the Matinan range ("nordseite der Matinang-Kette, etwa 1000 m hoch"), a skin and skull, which is also in the collection at Basel (see gazetteer). We have no idea where the other specimen is, the one collected between Kottabangon and Bolang Mongondo; it is not in Basel, Dresden, Leiden, or London.

SNSD B168, one of the two specimens from Gorontalo that Meyer (1896: 26) referred to by numbers and the one that Feiler (1999) regarded as the holotype, remains at Dresden (the other, 857, is no longer listed in the collection inventory; C. Stefen, in litt., 2008). It is currently identified in the inventory of mammal specimens at that institution, and on the skin and skull tags, as the "type" of *occidentalis* and the collection locality as "Gorontalo." Clara Stefen kindly sent us color images of the skin and skull. The slightly stuffed nearly flat skin is intact except for a long tear in the throat, and most of the tail is missing. In ventral view, three pairs of large teats are clearly evident. On the dorsal surface the black ear tufts are prominent but there is no discernable trace of nape patches behind the ears. The occiput and part of the basioccipital region of the skull are missing, the mandible is intact and all upper and lower teeth are present.

SNSD B168 was identified by Feiler (1999: 407) as the holotype of *occidentalis*, and the Matinan range as the type locality. The specimen (NMB 1198/9543) from the Matinan range, however, is at Basel where it was cataloged in 1942 and is a male; it cannot define the type locality if the Dresden squirrel is indeed the type. However, SNSD B168, a female, is to be regarded as the lectotype (see below). Since Meyer (1896: 26) had explicitly stated that it came from Gorontalo, the type locality changes accordingly. Sometime between the publication of Feiler's 1999 catalog of types and the present, the skin and skull of SNSD B168, the supposed holotype of *occidentalis* in Feiler's catalog, was correctly linked to its provenance, Gorontalo, in the museum inventory.

The identification as "holotype" assigned to SNSD B168 by Feiler (1999: 407) should have been "lectotype" if we interpret correctly Article 74.5 ("Lectotype designations before 2000," ICZN, 1999: 82): "In a lectotype designation made before 2000, either the term "lectotype," or an exact translation or equivalent expression (e.g.

"the type" [in this case, Feiler's use of the term "holotype"]), must have been used. ..."

In light of the above, the other specimens discussed by Meyer (1896: 26, 1898: 2) now become paralectotypes. These include the squirrel at Basel (NMB 1198/9543) collected on the north slopes of the Matinan range, and the following six specimens from Leiden: **(1)** specimen "*i*" (Jentink, 1888: 25), RMNH 39399, a mounted skin still containing the skull, male, from Tulabolo, near Gorontalo, northern Sulawesi, collected on May 10, 1864 by C.B.H. Rosenberg; **(2)** specimen "*j*" (Jentink, 1888: 25), RMNH 39400, a mounted skin with skull still inside, female, from Tulabolo, near Gorontalo, northern Sulawesi, collected on May 10, 1864, by C.B.H. Rosenberg; **(3)** specimen "*k*" (Jentink, 1888: 25), RMNH 39394, a mounted skin without skull, male, from Paguat, northern Sulawesi, collected between November 5–12 by E.A. Forsten (also a paralectotype of *P. leucomus*; see that account); **(4)** specimens "*l*" (the skin, in Jentink, 1888: 25) and "*h*" (the skull, in Jentink, 1887: 191), RMNH 39401, a mounted skin and cranium, male, from Panibi, near Gorontalo, northern Sulawesi, collected between September 7–15, 1863, by C.B.H. von Rosenberg; **(5)** specimen "*m*" (Jentink, 1888: 25), RMNH 39402, a mounted skin still containing the skull, female, from Medelido, near Gorontalo, northern Sulawesi, collected between May 9–20, 1863 by C.B.H. von Rosenberg; **(6)** specimen "*p*" (Jentink, 1888: 25), RMNH 39403, mounted skin still containing the skull, sex unknown, from Limboto, northern Sulawesi, collected during January, 1876, by S.C.J.W. van Musschenbroek.

Prosciurillus alstoni (Anderson, 1879)

Sciurus alstoni Anderson, 1879: 252, pl. xxi (1878 is imprinted on the title page of the book, but the Corrigenda on the following page proclaims "The sanguine expectation that this work would have been issued during the past year has led to 1878 appearing on the title-page instead of 1879, the delay having arisen from circumstances over which the author had no control.").

Sciurus tonkeanus Meyer, 1896: 25, pl. X, fig. 4.

Sciurus sarasinorum Meyer, 1898: 1 (1899: 21, pl.V).

Sciurus mowewensis Roux, 1910: 519.

Sciurus elbertae Schwarz, 1911: 639.

HOLOTYPE AND TYPE LOCALITY: The holotype of *Sciurus alstoni* (ZSI 9546) consists of a museum study skin and damaged skull and is an unsexed adult that was "purchased" (see Sclater, 1891: 21; Khajuria et al., 1977: 31). Some measurements are listed in table 14.

The type locality is the Malakosa region (northern portion of the central core of Sulawesi), Kuala Navusu, approximately 00°58′S, 120°27′E, in the coastal lowlands at 30 m, between Tanjung Pandendelisa (jutting into Teluk Tomini) and the mouth of Sungai Sausu to the southeast (locality 1 in gazetteer and identified on the maps in figures 11 and 17), Indonesia, Propinsi Sulawesi Tengah.

Our identification of the holotype of *alstoni* as a member of the *P. leucomus* group and selection of a type locality requires explanation, beginning with Anderson's (1879: 252) description of *Sciurus alstoni*, which is short but diagnostic (see also fig. 16):

> This beautiful species, in the colouring of the upper parts and tail, closely resembles *S. lokriah* [= *Dremomys lokriah*, endemic to Central Nepal, Assam, Burma and western Yunnan; Corbet and Hill, 1992: 298], whilst the under parts differ in being dusky chestnut instead of orange. The peculiarity of the species is the beautiful pure white tufting to the ears, which projects a considerable way backwards, in a pointed manner. The external surface of the tip of the ear is covered with short brown hairs which stand out against the white. The subapical brown, or rather black band of the hairs of the tail, is broad and rather deeply edged with whitish; the tip of the tail is blackish, and the remainder more or less obscurely tinged with black and orange.
>
> The incisors are pale yellow, and narrow; the facial portion of the skull is rather short and moderately pointed, and the nasals are rather broad posteriorly.

Anderson provided measurements for "Length, muzzle to tail [our Length of Head and Body]," as 7.15 in. (= 181.6 mm); "Length of tail without hair [our Length of Tail]," 6.50 in. (= 165.1 mm); and "Length of tail with hair," 8.30 in. (= 210 mm). We have no comparable standard measurement for length of tail including the terminal tuft, so

Fig. 16. Reproduction of Anderson's (1879) color plate of "*Sciurus alstoni*" (= *Prosciurillus alstoni*).

we measured the tail tufts of seven skins from Sungai Tolewonu and 19 skins from Kuala Navusu and added those values to lengths of tails (= tail vertebrae) for those specimens, obtaining the range 209–235 mm for the Tolewonu series, and 198–236 mm for the Navusu sample. As to the provenance of the specimen, Anderson wrote: "The locality from whence this species was obtained has not been accurately ascertained, but it is probably Borneo."

Anderson's *alstoni*, with a few exceptions, disappeared from published checklists of squirrel species (Agrawal and Chakraborty, 1979, for example; Thorington and Hoffmann, 2005, who did list an *alstoni*, proposed by J.J. Allen in 1889, but that *alstoni* is a synonym of *Sciurus nayaritensis*, a fox squirrel occurring in northern Mexico and the southwestern United States; see p. 762 in that publication), checklists of rodents focusing on those native to the Indomalayan region (Chasen, 1940, for example), and publications devoted to mammals of a particular geographic region in the Indomalayan area, especially Borneo and the Malay Peninsula (Moore and Tate, 1965; Medway, 1969, 1977; Payne et al., 1985; Corbet and Hill, 1992). An early exception is Jentink's (1883: 118) "List of the specimens of squirrels in the Leyden Museum" where he recorded that *Sciurus alstoni* was "Characterized by the beautiful pure white tufting to the ears, which projects a considerable way backwards." Jentink cited Anderson's description and noted that "no specimens were in the Leyden Museum." Another is an entry for *Sciurus alstoni* in Sclater's (1891: 21) catalog of mammals in the Indian Museum where he noted that "The type and only specimen known is said to have come from Borneo," indicating that a skin was present in the collection and that the specimen had been "purchased." In Ellerman's (1940: 376) compendium on the families and genera of living rodents, he listed *alstoni* as a species of *Callosciurus* in a category "*incertae sedis; not allocated to groups*." Another exception is Khajuria et al. (1977: 31) who provided "An annotated catalogue of the type specimens of mammals in the collections of the Zoological Survey of India [formerly the Indian Museum]," and entered information on the holotype of *Sciurus alstoni*. While Anderson (1879), Sclater (1891), and Ellerman (1940) noted the type locality to probably be "Borneo," Khajuria et al. (1977: 31) narrowed it to "Indonesia, Kalimantan" but gave no reasons for doing so.

The most recent and only insightful allocation of Anderson's *alstoni* was made by Corbet and Hill (1992: 304) in their systematic review of the mammals of the Indomalayan region. They listed the combination "? *Sciurus alstoni*" among the scientific names associated with *Prosciurillus leucomus*, the provenance as "locality unknown," and repeated Anderson's "probably Borneo."

We have not personally studied the holotype of Anderson's *Sciurus alstoni*. We contacted Dr. Sujit Chakraborty at the headquarters of the Zoological Survey of India who informed us that the holotype is present in the collection and kindly provided us with values for some cranial measurements. The measurements, along with Anderson's description, measurements of body and tail, and the superb color plate depicting the squirrel in live pose (reproduced in fig. 16) do not describe any species of squirrel, no matter the genus, that is native to Borneo, as anyone can determine by simply thumbing through the color plates of squirrels (pls. 23–30) and relevant pages of descriptive text (233–243) in Payne et al.'s (1985) field guide to the mammals of Borneo. We know of no other species of tropical Indomalayan squirrel occurring outside of Borneo and west of Sulawesi, or in the Philippines that bears close resemblance to "*Sciurus alstoni*" (see the color plates depicting species of Indomalayan squirrels from the Malay Peninsula [Medway, 1969], Thailand [Askins, 1988], and "Southeast Asia" [Francis, 2008]; the statement is also based on Musser's study of Indomalayan squirrels stored in North American, Asian, and European museums).

The animal described by Anderson and depicted in his color plate is a member of the *Prosciurillus leucomus* group and an unambiguous representative of the same species from which the samples collected by Fritz and Paul Sarasin and described as *sarasinorum* (Meyer, 1898) and *mowewensis* (Roux,

1910) were obtained (see section discussing synonyms). Specimens from Kuala Navusu and Sungai Tolewonu collected by Musser (in AMNH), the sample from Pinedapa obtained by H.C. Raven (in USNM), and the squirrels collected from the southeastern peninsula by G. Heinrich (in AMNH) represent the same species. Values for length of head and body (181.6 mm) and length of tail (165.1 mm) for the holotype of *alstoni* fall within the range of variation listed in table 15 for these variables in the sample from Kuala Navusu and Sungai Tolewonu; length of tail relative to head and body length (91%) is also comparable, as is length of tail including the tuft (see above). The highlights of Anderson's description—dusky chestnut underparts, prominent white ear tufts, subapical blackish bands of the tail hairs that are tipped with white, blackish tail tip and the rest of the tail tinged with black and orange—match Musser's material laid out in front of us from Kuala Navusu and Sungai Tolewonu as well as the two examples of *sarasinorum* shown in Meyer's (1899) color plate (see fig. 10). Anderson's color plate of *alstoni* (see fig. 16), except for the underparts that appear faded, rendered orange rather than "dusky chestnut," exhibits the same diagnostic pelage highlights described by him.

Where the holotype of *alstoni* was collected in Sulawesi is unknown. The specimen was purchased, according to Sclater (1891: 21) and Khajuria et al. (1977: 31), probably during Anderson's tenure as Superintendent of the Indian Museum, Calcutta (now the Zoological Survey of India, Kolkata), certainly before 1879. It had to have been collected within the range of the *Prosciurillus* exhibiting the *alstoni* pelage color pattern. Our voucher specimens characterized by that coloration and patterning come from lowlands and middle altitudes (31–1200 m) in the eastern portion of the central core of Sulawesi and throughout the mainland of the southeastern peninsula (see gazetteer and fig. 11). Forests of lowlands and mountains in the western portion of the central core are occupied by *P. topapuensis*, the distinctive *P. weberi* is found in lowlands at the southern sector of the central core west of the range of *alstoni*, and forests on the northern peninsula are inhabited by *P. leucomus* (see gazetteers and fig. 11).

There are two early travel routes in this range where the holotype of *alstoni* could have been collected. One extended from the Luwu region at the north end of Teluk Bone north to Mapane at the southern end of Teluk Tomini. Paul and Fritz Sarasin traveled this route in the late 1800s where they obtained a squirrel at Usu on the southern end and a specimen from Mapane at the northern end. The two specimens became the basis for Meyer's (1898) description of *Sciurus sarasinorum*. The other route transects the southeastern peninsula from Kolaka at Teluk Mekongga in the west to Kendari at the margin of Teluk Kendari in the east. The Sarasins traveled here in the early 1900s where they obtained the two specimens later described by Roux (1910) as *Sciurus mowewensis*. Earlier European travelers may have taken the same routes and possibly acquired Anderson's specimen along the way but we just do not know. The animal could even have been brought to Borneo by traders.

In the absence of any information about a collection locality for the holotype of *alstoni*, we turned to the International Code of Zoological Nomenclature (4th ed., 1999) for insight into selecting a type locality. One of the recommendations listed in that document (76A.1.4.) is pertinent here: "In ascertaining or clarifying a type locality, an author should take into account "as a last resort, and without prejudice to other clarification, localities within the known range of the taxon or from which specimens referred to the taxon had been taken."

Within what is the known range of *Prosciurillus alstoni* defined by voucher specimens, we select Kuala Navusu (approximately 00°58′S, 120°27′E) as the type locality for the taxon. This is one of Musser's camps where during August–November 1975, he obtained 26 specimens of *P. alstoni* in lowland tropical evergreen rain forest between 30 and 229 m (see gazetteer). The campsite and surrounding region where Musser surveyed was located between the village of Malakosa (behind Tanjung Pandendelisa jutting into Teluk Tomini) and the mouth of Sungai Sausu (fig. 17). *Prosciurillus alstoni* was common in the forest there and

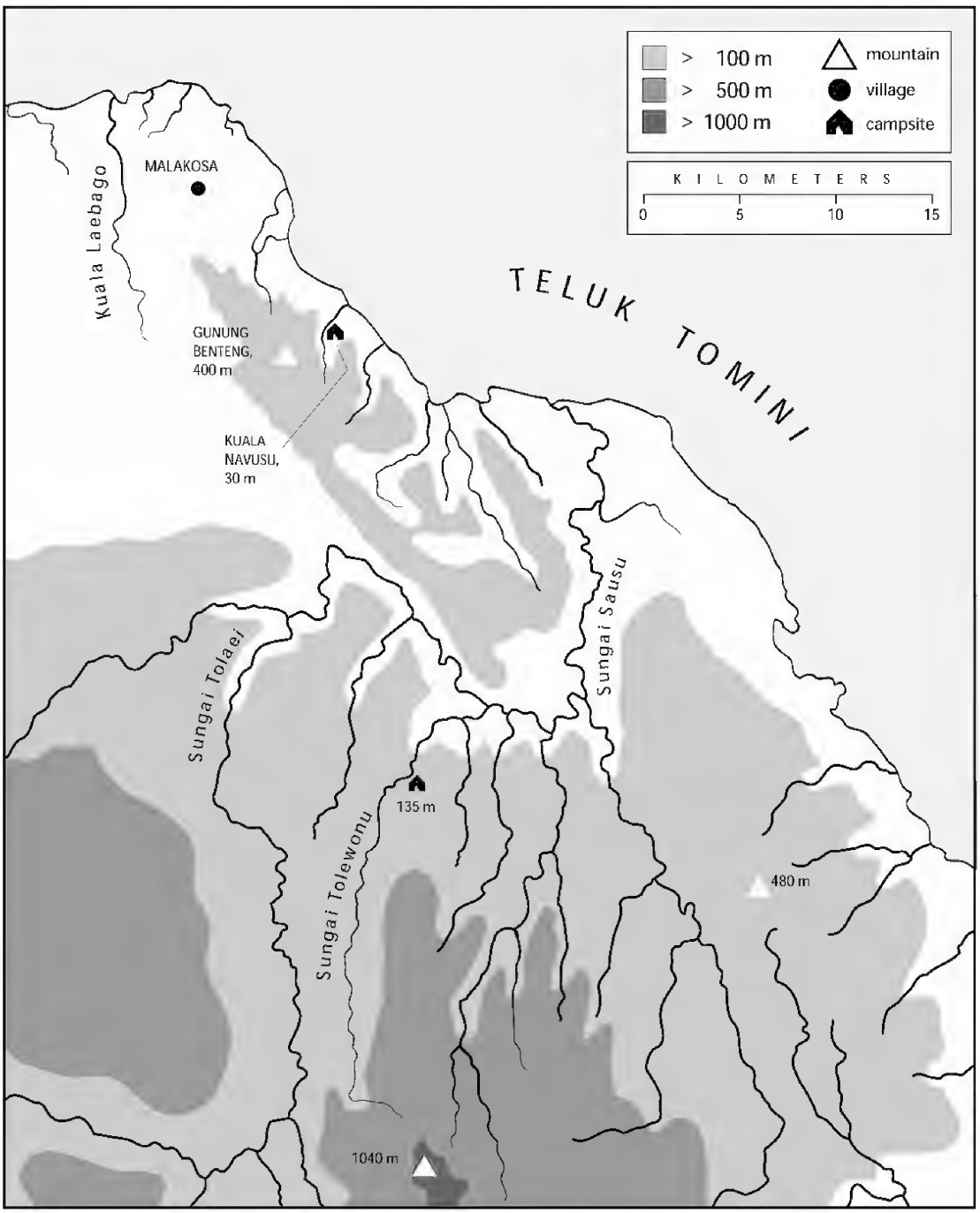

Fig. 17. The region south of Malakosa in Sulawesi's central core, which shows Musser's two lowland camps (Kuala Navusu, Sungai Tolewonu) in lowland tropical evergreen rain forest (see the map in fig. 3 for geographic orientation within the geographically broader northern portion of the central core). *Rubrisciurus rubriventer*, *Prosciurillus alstoni*, and *P. murinus* were common in this region; *Hyosciurus ileile* also occurs here but was infrequently encountered. We designated Kuala Navusu as the type locality of *Prosciurillus alstoni*.

also south of Kuala Navusu at Musser's camp on the Sungai Tolewonu (approximately 01°04′S, 120°27′E; fig. 17), one of the tributaries of Sungai Sausu, where during January and February 1976 he collected 16 specimens between 122 and 366 m (see gazetteer). The specimens from both places match Anderson's (1879) description of "*Sciurus alstoni*" in all aspects of body dimensions and pelage coloration.

EMENDED DIAGNOSIS: *Prosciurillus alstoni* shares with other members of the *P. leucomus* group moderate body size and a tail equal to or shorter than length of the head and body (tables 2, 14, 15). It contrasts with the other four species in the group by the following combination of pelage traits (see table 12): **(1)** dorsomedial surface of each ear covered with long white hairs projecting beyond ear rim to form a prominent tuft on most specimens, ears without tuft and concolorous with head and neck in a few individuals; **(2)** no bright ochraceous hairs lining inside of the pinnae, which is same color as fur on neck and head; **(3)** no nape patches behind the ears; **(4)** no middorsal black stripe extending along back from neck to base of tail; **(5)** dark reddish brown (approaching chestnut) underparts; and **(6)** a geographic range restricted to tropical lowland evergreen rainforest habitats on the eastern portion of Sulawesi's central core, the east-central peninsula, the southeastern peninsula, and islands offshore of that arm.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: Collection localities of *P. alstoni* are from the eastern portion of Sulawesi's central core, the southern coastal plain on the east-central peninsula, the southeastern peninsula, and the islands of Buton and Kabaena (see gazetteer and map in figure 11). Collection sites range in elevation from 30 m (Kuala Navusu and Pinedapa) to 1200 m (Sungai Tolewonu), all in lowland tropical evergreen rainforest habitats (fig. 17). The distribution of collection sites indicates that *P. alstoni* is not sympatric with any other member of the *P. leucomus* group. The most northern record of *P. alstoni* is Kuala Navusu (00°58′S, 120°27′E). Approximately 100 km north of there is Bumbarujabu (00°43′S, 120°04′E) at the base of the northern peninsula and the southernmost collection locality for *P. leucomus* (see gazetteer and fig. 11). Between those two places along the eastern coast, assuming the presence of intact forest, the ranges of *P. leucomus* and *P. alstoni* either overlap (likely narrowly) or are parapatric. The pattern of contact is unknown because no members of the *P. leucomus* group have been collected along that coastal strip.

The mountains south of Bumbarujabu and west of Danau Poso in the western half of Sulawesi's central core—west of the range of *P. alstoni*—are inhabited by *P. topapuensis*, another member of the *P. leucomus* group. The boundaries of each range in that vast region of central Sulawesi between Teluk Tomini in the north and Teluk Bone in the south are unknown because no voucher specimens are available from there (see map in fig. 11). Members of the *P. leucomus* group have been collected only in the coastal lowlands bordering Teluk Tomini and lowlands around Teluk Bone. In the northern lowlands, samples of *P. alstoni* are from Mapane (01°26′S, 120°40′E) on the coast and inland a bit at Pinedapa (01°25′S, 120°35′E), 31 m. Westward toward the mountains, approximately 20 km from Pinedapa, is Rano Rano (01°30′S, 120°28′E), 1829 m, the easternmost collection site for *P. topapuensis* (see gazetteer and fig. 11). In this region, and possibly farther south along flanks of the mountains, *P. topapuensis* may occur only in montane forest formations (although it descends much lower, down to 350 m, in the western part of its range) and *P. alstoni* in lowland evergreen rain forests; only results from future surveys will provide a description of the boundary between these two species.

Southern lowlands fringing Teluk Bone have yielded two species in the *P. leucomus* group. *Prosciurillus alstoni* has been collected at the base of the southeastern peninsula at Usu (02°36′S, 121°06′E), and Masamba (02°34′S, 120°19′E), about 80 km west of Usu, is the easternmost collection site for *P. weberi*. Whether the two species overlap or their ranges abut in this lowland interval is unknown.

Prosciurillus alstoni may be restricted to habitats in tropical lowland evergreen rain forests. While *P. leucomus*, its northern

neighbor, ranges from coastal lowlands to habitats in montane forest (coast to 1700 m), and *P. topapuensis*, its western relative, extends from tropical lowland forests at 350 m to upper montane formations at 2800 m, *P. alstoni* has yet to be collected above 1200 m (table 4). Montane areas within its range, however, have received little or no survey focusing on collections of small mammals with the exception of Pegunungan Mekongga in the southern portion of the southeastern peninsula. Samples of *P. alstoni* come from Wawo (03°41′S, 121°02′E) 50 m, on the coast west of that mountain range and Masembo (03°35′S, 121°15′E) on the lower flanks of the range at 550 m, all collected by G. Heinrich in the early 1930s. At higher elevations in lower and upper montane rainforest formations, Heinrich encountered only *Rubrisciurus rubriventer* (1400 m) and *Prosciurillus abstrusus* (1500 and 2000 m). He was an able naturalist and skilled hunter, daily walking the forests shooting birds and squirrels for various museums, and likely would have collected examples of *P. alstoni* if it occurred at elevations higher than 550 m.

Much remains to be learned about the actual geographic range of *P. alstoni*. Its distribution on the east-central peninsula, for example, is a mystery; specimens are from only a single locality on the southern coast, but the species probably occurs throughout the lowlands fringing the mountainous backbone of the peninsula. Whether *P. alstoni* or some other member occurs in the mountains is unknown; it is possible a member of the *P. leucomus* group is absent from high altitudes on the peninsula, a pattern that would resemble that seen on Pegunungan Mekongga. The nature of the contact zones between the range of *P. alstoni* and those of *P. leucomus* to the north and *P. topapuensis* and *P. weberi* to the west are enigmas. Surveys in the east-central peninsula and through relevant regions in the central core of Sulawesi are needed to refine the geographic distribution of *P. alstoni* and its distributional pattern relative to the other three species.

A segment of *P. alstoni*'s range matches that of the macaque, *Macaca ochreata*. That monkey has been recorded from the islands of Buton and Muna, and from the mainland of the southeastern peninsula north to the lakes region (Danau Towuti, Danau Mahatona, and Danau Matana). In landscapes north of the lakes in the east-central peninsula and the central core of Sulawesi, *M. ochreata* is replaced by *M. tonkeana* (Fooden, 1969; Groves, 2001, 2005). *Prosciurillus alstoni* also occurs on the islands and mainland south of the lakes region, but as opposed to *Macaca ochreata*, it ranges farther north into the east-central limb and to the northeastern portion of the central core.

DESCRIPTION: *Prosciurillus alstoni* is similar to *P. leucomus* in body size, with the tail averaging as long as, or only slightly shorter than, the length of head and body as in that species (length of head and body, 157–195 mm; length of hind foot, 40–48 mm; length of ear, 15–19 mm; weight, 135–210 g; see table 15). Thickness and color of the fur covering upperparts of head and body are also similar; both possess a uniformly thick (12–15 mm) coat that is dark brown flecked with black and orange along midline of the body from forehead to base of tail, but grading into brownish gray spotted with black and pale buff along sides of the head, body, forelegs, and hind legs. Dorsal surfaces of the front and hind feet may be the same color as the head and back, slightly darker, or slighter paler (buffy gray) in both species. Coloration of the body fur results from the mixture of dark gray curly underfur; longer overfur composed of black hairs, each blackish gray interrupted by a subterminal orange or pale buffy band and black tip; and black guard hairs barely projecting beyond the overhair layer. Cheeks range from buffy to ochraceous.

The dorsal background forming the upperparts of *P. alstoni* is interrupted by color patterning on the head and ears. Top and sides of the muzzle are ochraceous, a pattern also seen in *P. leucomus*. Unlike that species, however, *P. alstoni* lacks any sign of nape patches behind the ears—fur over the neck is indistinguishable in color from that covering the rest of the upperparts. *Prosciurillus alstoni* also lacks the prominent black ear tufts and ochraceous inner ear lining characteristic of *P. leucomus*. Instead, the hairs covering most of each ear on *P. alstoni* are similar in coloration to the head and body, a

small black tuft sits at the inner dorsal margin of the ear, and from the medial surface springs a conspicuous white tuft that projects 5–8 mm beyond the dorsal curvature of the ear. The visual pattern evolves around an ear with a dab of black on the inner surface and rimmed by a white crest (see the color plates in figs. 10, 16). The white tufting is variable in expression both within and between samples; it is whitish buff in some specimens and absent from others. This variation is more fully explored in the sections discussing geographic variation and synonyms.

The short (5–7 mm thick) ventral coat of *P. alstoni* is deep, dark red—bordering on reddish brown or chestnut—on most specimens; some individuals from the southeastern peninsula have reddish orange or orange-red venters. The hairs forming the ventral covering are dark gray along their basal half and deeply pigmented with red or reddish orange along the distal half.

The tail of *P. alstoni* is equal to or slightly shorter than length of head and body (LT/LHB = 89%–99%, see table 15) and is covered in long hairs, each patterned by alternating black and buffy or orange bands. The overall effect is rings of black and buff with buffy bands outlining margins of the tail and long black hairs forming a black terminal tuft. The ventral surface of the tail is reddish (paralleling the venter coloration) bordered by black and buffy margins. Overall coloration of the tail is closely similar to that seen in *P. leucomus*.

Females have three pairs of teats, one postaxillary pair, and two inguinal pairs. A single embryo was found in each of the few pregnant squirrels examined.

Views of the skull are illustrated in figures 12–14; cranial and dental measurements are summarized in tables 16 and 19.

COMPARISONS: *Prosciurillus alstoni* requires comparisons with *P. leucomus*, endemic to the northern peninsula north of the distribution of *P. alstoni*; *P. weberi*, known only by specimens from the lowlands fringing Teluk Bone west of the range of *P. alstoni*; and *P. topapuensis*, inhabiting the mountainous western portion of the central core to the west of *P. alstoni*.

***Prosciurillus alstoni* and *P. leucomus*:** Both species are similar in body size and length of tail relative to length of head and body (table 15), in coloration of the fur covering head and body, legs, dorsal surfaces of front and hind feet, and color and patterning over the tail. Both share an ochraceous muzzle. Both show bright underparts but those of *P. alstoni* are typically more deeply pigmented, dark reddish brown as opposed to orange-red on average in *P. leucomus* (reddish orange to ochraceous is the chromatic range). Other pelage dissimilarities are striking (table 12): *P. alstoni* lacks any indication of nape patches behind the ears, a pattern characteristic of most examples of *P. leucomus*; and the ears are either adorned with a prominent white tuft or lack such a tuft in which case the ears, including the inner surfaces, are the same color as the head and neck—all specimens of *P. leucomus* exhibit prominent black ear tufts and bright ochraceous inner ear surfaces beneath the tufts.

The two species are not so different in cranial and dental dimensions (table 17) but significant proportional differences exist, which are reflected in the ordination of specimen scores projected onto first and second principal components extracted from principal-components analysis shown in figure 18. No marked separation among the scores into two discernable clusters exists along the first axis, where the spread is influenced by covariation in all of the dimensions measured except mastoid breadth and height of braincase; breadth of rostrum and lengths of nasals, rostrum, and diastema have somewhat more impact (table 20).

The points separate into two overlapping clusters along the second component, reflecting the relatively slightly smaller skull, shorter tooth rows, but wider rostrum and longer diastema in *P. alstoni* compared to *P. leucomus*. These distinctions, while not immediately evident when comparing the descriptive statistics for each dimension in the two samples (tables 17, 19), can be appreciated visually by comparing side-to-side adult skulls with a comparable degree of wear on the teeth. *Prosciurillus alstoni* generally has a smaller skull and shorter tooth rows than *P. leucomus*.

TABLE 19
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Separate Population Samples of *Prosciurillus leucomus* and *Prosciurillus alstoni*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	*P. leucomus* northeastern peninsula $N = 18$	*P. leucomus* northern peninsula $N = 8$	*P. alstoni* central core, Malakosa region $N = 32$	*P. alstoni* central core, Pinedapa $N = 19$	*P. alstoni* southeastern peninsula $N = 11$
ONL	45.6 ± 0.73 (44.1–46.8)	46.1 ± 0.90 (44.8–47.6)	44.5 ± 0.77 (42.6–46.5)	44.5 ± 0.73 (43.1–46.0)	44.2 ± 1.20 (42.0–45.7)
CBL	41.1 ± 0.95 (39.8–43.8)	41.6 ± 1.13 (39.6–42.6)	39.9 ± 1.03 (37.8–43.3)	39.5 ± 0.75 (38.5–41.6)	40.0 ± 0.68 (38.8–40.9)
ZB	27.7 ± 0.61 (26.8–29.0)	28.4 ± 0.85 (27.2–29.5)	27.5 ± 0.64 (26.1–28.8)	26.8 ± 0.71 (25.4–27.7)	27.4 ± 1.13 (25.7–29.1)
IB	17.6 ± 0.56 (16.7–18.8)	17.8 ± 0.50 (16.9–17.8)	17.2 ± 0.77 (15.2–19.1)	17.2 ± 0.63 (16.2–18.3)	17.0 ± 0.66 (15.4–18.0)
LN	12.7 ± 0.58 (11.7–13.7)	12.9 ± 0.68 (12.1–14.0)	12.5 ± 0.55 (11.5–13.9)	12.2 ± 0.44 (11.4–13.0)	12.1 ± 0.51 (11.2–12.8)
LR	20.3 ± 0.62 (19.2–21.2)	21.0 ± 0.94 (19.7–22.2)	19.9 ± 0.63 (18.3–21.3)	19.4 ± 0.47 (18.7–20.3)	19.6 ± 0.70 (18.5–20.6)
BR	8.5 ± 0.54 (7.3–9.5)	8.9 ± 0.66 (8.0–9.9)	8.5 ± 0.43 (7.7–9.4)	8.5 ± 0.53 (7.6–9.4)	8.3 ± 0.69 (7.6–9.6)
MB	19.2 ± 0.39 (18.4–20.0)	19.4 ± 0.46 (18.9–20.1)	19.1 ± 0.38 (18.3–19.8)	19.3 ± 0.39 (18.6–19.9)	19.7 ± 0.54 (18.6–20.5)
HBC	15.1 ± 0.44 (14.0–15.7)	15.3 ± 0.53 (14.7–16.3)	14.9 ± 0.40 (14.2–15.6)	15.2 ± 0.39 (14.5–15.8)	14.8 ± 0.41 (14.2–15.5)
LO	10.5 ± 0.24 (10.0–11.0)	10.4 ± 0.48 (9.7–10.9)	10.2 ± 0.30 (9.7–11.0)	10.2 ± 0.27 (9.8–10.8)	9.8 ± 0.50 (8.6–10.4)
LD	8.9 ± 0.37 (8.1–9.5)	9.2 ± 0.51 (8.4–10.0)	9.1 ± 0.37 (8.4–10.1)	8.7 ± 0.40 (8.0–9.7)	8.8 ± 0.49 (8.2–9.7)
LBP	12.4 ± 0.44 (11.5–13.1)	12.8 ± 0.53 (12.1–13.5)	12.6 ± 0.41 (11.7–13.5)	12.4 ± 0.32 (11.8–13.1)	12.3 ± 0.27 (11.9–12.7)
PPL	17.7 ± 0.39 (17.0–18.4)	17.6 ± 0.43 (16.7–18.0)	17.1 ± 0.68 (15.3–19.1)	17.4 ± 0.56 (16.4–18.7)	17.1 ± 0.60 (15.8–17.7)
BBP	10.0 ± 0.25 (9.5–10.5)	10.0 ± 0.37 (9.4–10.4)	9.5 ± 0.27 (9.0–10.4)	9.6 ± 0.35 (9.6–10.1)	9.5 ± 0.50 (8.6–10.4)
LB	8.1 ± 0.26 (7.7–8.7)	8.0 ± 0.11 (7.8–8.1)	8.0 ± 0.29 (7.4–8.5)	7.9 ± 0.20 (7.2–8.0)	7.9 ± 0.45 (7.1–8.6)
CLPMM	7.8 ± 0.24 (7.1–8.0)	7.6 ± 0.17 (7.3–7.8)	7.2 ± 0.18 (6.8–7.5)	7.2 ± 0.26 (6.7–7.8)	7.2 ± 0.22 (6.9–7.6)

Although the morphometric distinctions between the two species are subtle, the contrasts in color pattern are not. While not every example of *P. alstoni* has white ear tufts, none exhibits black ear tufts, and not one of the specimens we examined has nape patches behind the ears. These traits, along with their average darker red underparts and proportionately smaller skull and tooth rows, set *P. alstoni* apart from *P. leucomus*.

Prosciurillus alstoni* and *P. weberi: Our sample of *P. weberi* consists of eight individuals collected at two localities, with only five yielding a full set of cranial and dental measurements. If the two collection sites, in lowlands (100 m or less) fringing the northwestern margin of Teluk Bone, are representative of the altitude of *P. weberi*—namely tropical lowland evergreen rainforest habitats—then both *P. weberi* and *P. alstoni* share this lowland habitat affinity. The northern peninsular *P. leucomus* occurs through a range of forest formations from the coastal lowlands to montane habitats, and the west-central *P. topapuensis* inhabits mountain forests but in places ranges into lowlands.

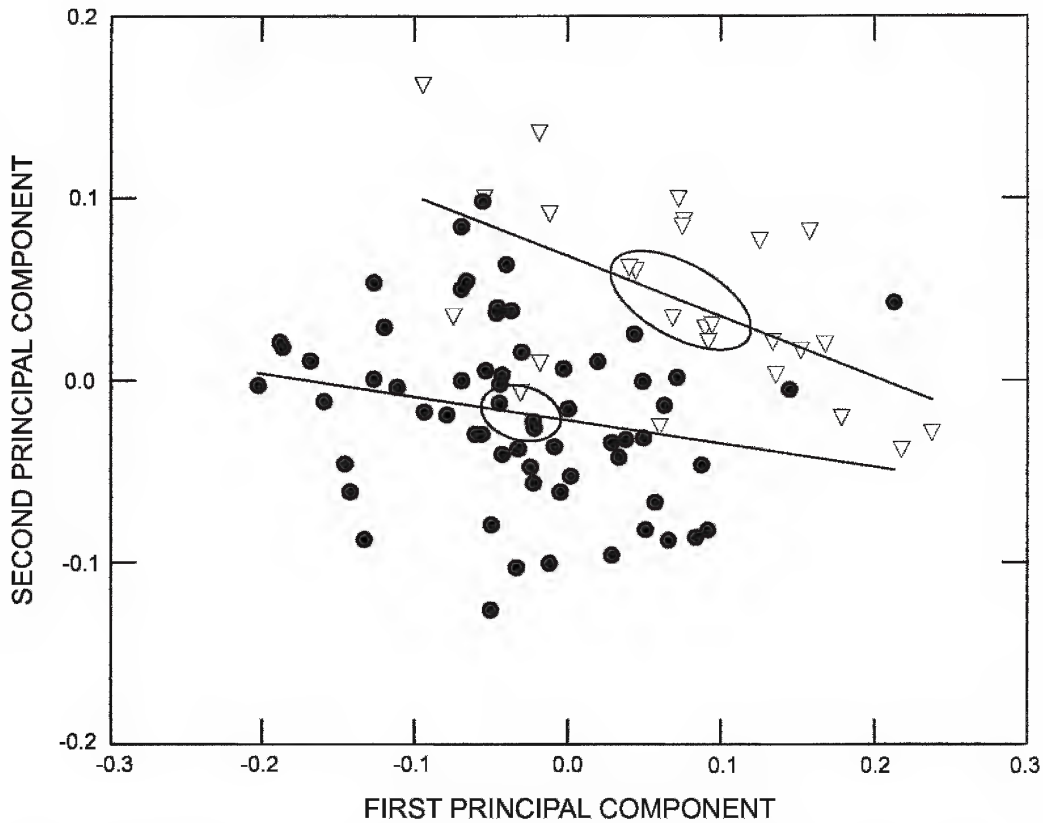

Fig. 18. Specimen scores representing population samples of *Prosciurillus leucomus* from the northern peninsula (empty inverted triangle, $N = 26$) and *P. alstoni* from the central core and southeastern peninsula (filled circle, $N = 63$) projected onto the first and second principal components extracted from principal-components analysis. The ellipses outline 95% confidence limits for the specimen scores forming each cluster. Equations for the regression lines are: *P. leucomus*, $Y = -0.331X+0.068$ ($F = 11.30$, $P = <0.01$); *P. alstoni*, $Y = -0.133X-0.023$ ($F = 3.42$, $P = 0.059$). Each regression line of the second principal component on the first component is clearly distinct from the other; while their Y-intercepts are significantly different (+0.068 versus −0.023; $F = 13.02$, $P = 0.001$), their slopes are not (−0.331 versus −0.133F = 2.53, $P = 0.12$). See table 20 for correlations and percent variance.

Measurements of head and body, tail, hind feet, and ear from specimens of *P. weberi* are scanty but do indicate a close resemblance to *P. alstoni*, and other members of the *P. leucomus* group, in body size (tables 15, 16, and 17). *Prosciurillus alstoni* also closely resembles *P. weberi* in coloration of fur covering upperparts and underparts, as well as color and patterning on the tail. The striking differences between the two species involve markings on the back and ears. Although the background color of fur over the back is similar in both, that of *P. weberi* is broken by a "broad black band along the spine of the back, running from the neck, increasing in broadness in the middle of the back and diminishing towards the root of the tail," as Jentink (1890: 116) described it. This dorsal pattern marks every specimen of *P. weberi* we studied but is absent from all examples of *P. alstoni* examined. Black tufts adorn the ears of *P. weberi* but comparable tufts in *P. alstoni* are white or not present (table 12). Jentink (1890: 116) noted that in one of the specimens of *P. weberi* he examined, "the black earpencils are slightly tipped with white."

Our available samples from which we derived morphometric data for analyses are unsatisfactorily uneven: 63 skulls of *P. alstoni*

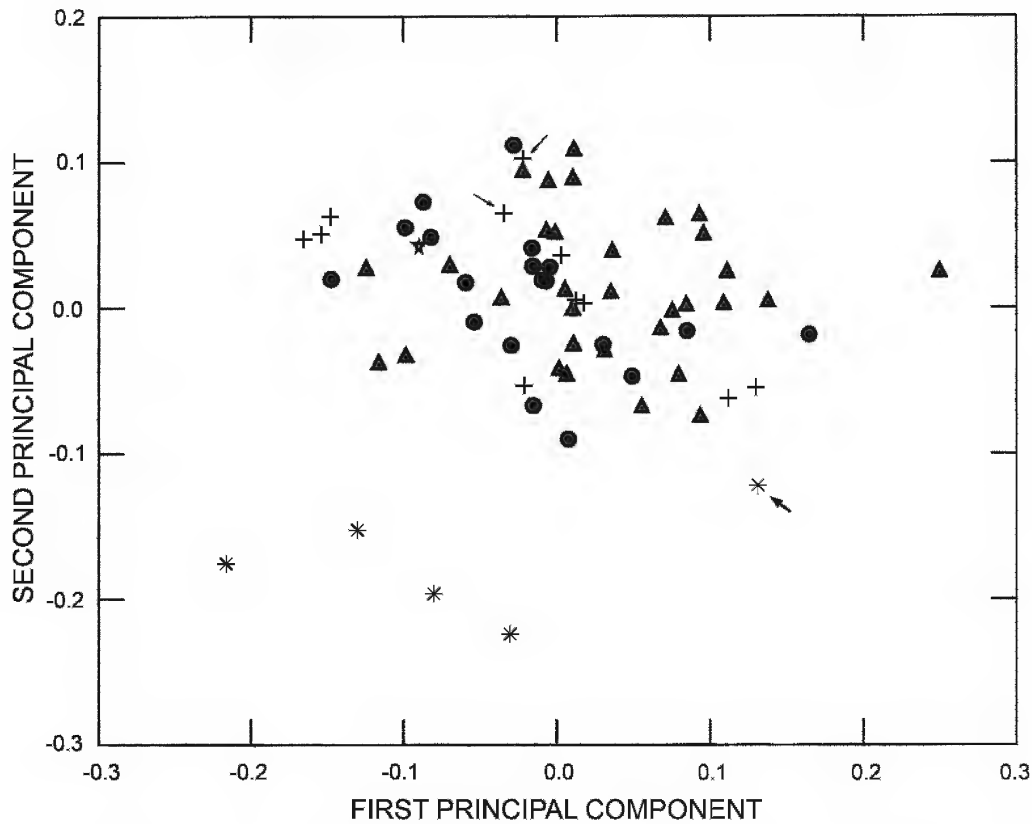

Fig. 19. Specimen scores representing population samples of *Prosciurillus alstoni* and *P. weberi* (8-pointed star; $N = 5$) projected onto the first and second principal components extracted from principal-components analysis. Symbols identifying samples of *P. alstoni* are: filled circle = Pinedapa, $N = 19$; filled triangle = Kuala Navusu and Sungai Tolewonu, $N = 32$; cross = southeastern peninsula, $N = 11$; star = Usu, lectotype of *sarasinorum*. Heavy arrow identifies score for the holotype of *weberi*; delicate arrows point to lectotype (top) and paralectotype (bottom) of *mowewensis*. See table 21 for correlations and percent variance.

but only five from *P. weberi*. Results we present here must be tested by employing a larger sample of *P. weberi*. Mean values for most cranial dimensions in the sample of *P. weberi* are smaller than comparable dimensions in the larger sample of *P. alstoni* (table 17). These distinctions are transformed visually in the ordination showing specimen scores projected onto the first and second principal components extracted from principal-components analysis in figure 19. There the large cloud of scores representing *P. alstoni* overlaps the smaller group of points for *P. weberi*. Covariation in all cranial and dental dimensions except height of braincase contributed to the spread of scores along the first principal component (table 21). The center of the larger constellation of points lies to the right of the smaller cluster, reflecting the overall average greater cranial and dental dimensions of *P. alstoni* compared to *P. weberi*.

The scatter along the second principal component results in separation of the specimen scores for *P. weberi* from the larger cloud formed by the sample of *P. alstoni*, and is a measure of distinctions in cranial and dental proportions. Highlighted is the relatively narrower skull and interorbital region of *P. weberi* compared with *P. alstoni*, its relatively shorter nasals and rostrum, lower braincase, smaller bullae, and shorter tooth row, but wider rostrum and longer diastema and postpalatal

TABLE 20
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus alstoni* with Those of *Prosciurillus leucomus*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 18.

Variable	PC1	PC2
ONL	0.018	0.005
CBL	0.024	0.007
ZB	0.021	−0.002
IB	0.025	0.003
LN	0.034	0.012
LR	0.032	0.006
BR	0.044	−0.038
MB	0.006	0.000
HBC	0.001	0.008
LO	0.016	0.009
LD	0.034	−0.011
LBP	0.017	−0.005
PPL	0.022	0.009
BBP	0.022	0.014
LB	0.010	0.005
CLPMM	0.019	0.029
Eigenvalues	0.009	0.003
Percent variance	381.912	13.520

TABLE 21
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus alstoni* with the Sample of *Prosciurillus weberi*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 19.

Variable	PC1	PC2
ONL	0.013	−0.001
CBL	0.020	0.003
ZB	0.025	0.010
IB	0.029	0.022
LN	0.035	0.015
LR	0.027	0.009
BR	0.032	−0.054
MB	0.007	0.005
HBC	0.001	0.011
LO	0.015	0.006
LD	0.032	−0.014
LBP	0.020	0.006
PPL	0.016	−0.007
BBP	0.015	−0.003
LB	0.017	0.008
CLPMM	0.009	0.019
Eigenvalues	0.008	0.005
Percent variance	31.599	19.775

region (table 21). Mean skull length is not so different in the two species (table 17), but many of the internal dimensions are less for *P. weberi* relative to those dimensions in skulls of *P. alstoni*, especially interorbital breadth and toothrow length, and three internal dimensions are of relatively greater magnitude.

Prosciurillus alstoni* and *P. topapuensis: These two species are dissimilar in altitudinal distributions, coat color and patterning, and cranial proportions. *Prosciurillus alstoni* inhabits tropical lowland evergreen rain forests and has not been collected above 1200 m within its range, which is east of the distribution for *P. topapuensis* (see map in fig. 11). That species is endemic to the western mountains and foothills of central Sulawesi and ranges through a variety of old-growth forest habitats, from tropical lowland evergreen rain forest to upper montane rain forest (table 4).

The species resemble each other in physical size with the exception that across geographic samples, *P. topapuensis* typically has a tail that is absolutely shorter and shorter relative to head and body length, and larger ears (tables 15, 16). Most *P. topapuensis* have thicker fur, especially samples from high altitudes; the dorsal coat of specimens from low altitudes is inseparable in color from upperparts of *P. alstoni*, but individuals from higher altitudes show a duller fur: the colored bands are mostly buffy instead of orange and buff. Tails of the two are similar in coloration and pattern of hair bands.

The striking dissimilarities between the two species involve the underparts and ears. All examples of *P. topapuensis* we examined have dark gray underparts lightly washed with buffy or ochraceous hues, or tinted silver, which contrasts strikingly with the dark reddish to reddish brown venters so characteristic of *P. alstoni*. Black tufts mark the ears on *P. topapuensis*. These are not as prominent as seen in some samples of the northern peninsular *P. leucomus*, and the variation in expression ranges from conspicuous tufts to just a trace of black so the ears are covered with the same color fur as the head and neck. No example of *P. topapuensis*

has white ear tufts, which is usual in *P. alstoni* (table 12).

Skulls of the two species are similar in overall size and in many internal cranial dimensions but differ in dimensional proportions. The correspondence in size is indicated by the mean values listed in table 17 and reflected in the graph of specimen scores projected onto first and second principal components extracted from principal-components analysis shown in figure 20. No separation of scores into discrete clusters is evident along the first component where all but two variables load positively (height of braincase and length of tooth row are the exceptions) and contribute to the the spread of points. Fewer variables load strongly along the second principal component but they point to significant differences in shape between the two species (table 22). Compared with *P. topapuensis*, the skull of *P. alstoni* is relatively wider (as indexed by zygomatic, interorbital, and mastoid breadths) and the orbit and ectotympanic bullae relatively longer; the nasals, diastema, and tooth row are relatively shorter, and the rostrum narrower.

GEOGRAPHIC VARIATION: Specimens of *P. alstoni* generally look alike no matter where they were obtained throughout the geographic range of the species as indicated by our samples at hand (tables 14, 19). The notable variation we see among adults involves the ear region. Ears of the nine specimens in the type series of *tonkeanus* from Tonkean on the east-central peninsula of Sulawesi (see gazetteer and fig. 11) have only short buffy hairs fringing their margins (clearly rendered in Meyer's, 1896, plate [reproduced in fig. 9] and evident in the color images of the type series given to us by Clara Stefen) and lack the characteristic white ear tufts seen in samples elsewhere within the range of *P. alstoni*; backs of the ears are covered with dark buffy hairs, which reach the rim of the pinna but do not project beyond it to form a tuft in most specimens, and form a short tuft in others. Otherwise, color of the upperparts, underparts, and tail of individuals in the Tonkean series match our samples from the central core of the island and the southeastern peninsula. No other samples of the squirrel have been collected from the east-central peninsula so we do not know whether the absence of white tufts is fixed in the population there, is individually variable at other localities, or if presence or absence of the white tufts shows a geographic pattern over the peninsula.

Our samples of *P. alstoni* elsewhere within its range exhibit variation in frequency of ear tufts and slight variation in color. In the central core of the range, three of the 24 skins from Kuala Navusu have short, inconspicuous whitish buff or buffy white tufts. Backs of the ears are covered with buffy white hairs that project 1–2 mm beyond the ear rims. The remaining specimens support a white coat over the medial surface of each ear, and the white hairs project from 3 mm to 8 mm beyond the ear rim. Individuals with the longer tufts match Anderson's color plate of *alstoni* (fig. 16) and Meyer's portrait of *sarasinorum* (fig. 10). One of the 12 skins from Sungai Tolewonu exhibits an inconspicuous, short buffy white tuft—nearly a fringe—but the others sport white tufts, the range in length comparable to that of the sample from Kuala Navusu. Of the 23 specimens from the southeastern peninsula (Wawo, Masembo, and Lalolei), one lacks tufts, back of the ears are dark buff with the hairs forming a low buffy fringe on the rim of the pinna (closely similar to the type series of *tonkeanus*); backs of the ears are buffy in seven individuals, with the hairs projecting 2 mm beyond to form an inconspicuous, short buffy tuft or high fringe; 18 specimens have prominent white tufts, the range in length comparable to that of the samples from Kuala Navusu and Sungai Tolewonu.

Two adult skins and skulls (MZB 6250 and 6251) from Pulau Buton are insular examples of *P. alstoni* (if Buton is the actual provenance) and were discussed by Sody (1949: 107) under "*Callosciurus tonkeanus*." Musser examined and compared the pair with AMNH specimens of *P. alstoni* collected at several places (Wawo, Masambo, and Lalolei) on the southeastern peninsula. In size and configuration of the skull, body size and proportions of appendages, and general coloration of fur covering body and tail, the two squirrels from Buton are similar to samples of *P. alstoni* from the mainland of the southeastern peninsula, and differ only in

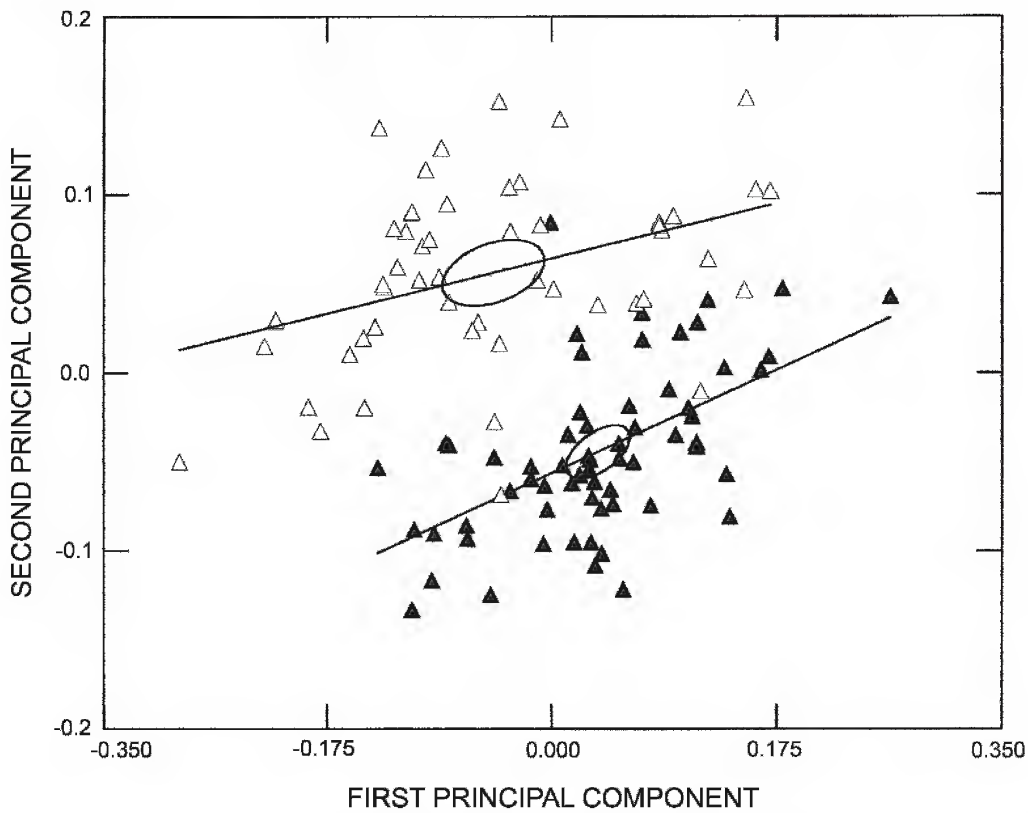

Fig. 20. Specimen scores representing population samples of *Prosciurillus alstoni* from the eastern segment of central Sulawesi and the southeastern peninsula (filled triangle, $N = 63$) and *P. topapuensis* from the mountainous western half of the central core of the island (empty triangle, $N = 50$) projected onto the first and second principal components extracted from principal-components analysis. The ellipses outline 95% confidence limits for the specimen scores forming each cluster. Equations for the regression lines are: *P. leucomus*, Y = 0.332X−0.056 (F = 26.56, P = <0.01); *P. alstoni*, Y = 0.176X+0.064 (F = 7.99, P = <0.01). Each regression line of the second principal component on the first component is clearly distinct from the other; while their Y-intercepts are significantly different (−0.056 versus +0.064; F = 31.49, P = <0.001). their slopes are not (0.332 versus 0.176; F = 2.97, P = 0.087). See table 22 for correlations and percent variance.

expression of the ear tufts. Instead of showing the tall and conspicuous tufting seen in most *P. alstoni*, the two individuals from Buton have less prominent tufts and they are white tinged with buff, matching some specimens from the central core and southeastern peninsular mainland described above. AMNH 101327, for example, from Lalolei, on the mainland, has short, whitish buff ear tufts; in this aspect and overall pelage color and patterning, the specimen is indistinguishable from the two Buton squirrels—although collected from different places at different times, all three squirrels could have been part of the same litter.

Multivariate analyses of cranial and dental variables among our geographic samples (identified in table 1) of *P. alstoni* drawn from the eastern section of Sulawesi's central core and the southeastern peninsula do not identify geographic components of the variation in these variables. The scatter of specimen scores projected onto first and second principal components extracted from principal-components analysis shown in figure 21 forms one large cloud in which are intermingled the points representing squirrels in the three geographic population samples. In addition to not revealing significant internal structure that correlates with geo-

TABLE 22
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus alstoni* with Those of *Prosciurillus topapuensis*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 20.

Variable	PC1	PC2
ONL	0.019	0.006
CBL	0.023	0.009
ZB	0.025	−0.007
IB	0.040	−0.030
LN	0.020	0.027
LR	0.029	0.009
BR	0.028	0.037
MB	0.023	−0.018
HBC	−0.002	0.004
LO	0.030	−0.021
LD	0.035	0.016
LBP	0.024	0.002
PPL	0.029	0.004
BBP	0.008	0.006
LB	0.032	−0.017
CLPMM	−0.000	0.013
Eigenvalues	0.010	0.005
Percent variance	35.853	17.027

graphic origin of the samples, the ordination also expresses individual variation within an age class, and variation associated with age since the range from young adults to old adults comprise each sample. Covariation in most cranial variables contributed to the spread of scores along the first axis (size), fewer load heavily on the second component (shape; table 23). Missing from this analysis is the sample from Tonkean, which consists of skins only.

ECOLOGY: *Prosciurillus alstoni* inhabits the upper canopy of primary tropical lowland evergreen rain forests, traveling through this layer along the pathways formed by the interlaced branches and woody vines. At gaps in the canopy squirrels descend to the ground where they bound along tree trunks and limbs lying on the forest floor and cross streams and rivers on bridges formed by branches of live trees arching over the water as well as rotting tree and palm trunks and tree limbs connecting opposite stream terraces. Most of the specimens Musser collected at the Kuala Navusu and Sungai Tolewonu areas were trapped on limbs of live trees growing over water or on rotting trunks and treefalls bridging streams (see summary of habitats at trapping sites in table 24, and photographs of forest in figs. 8, 22, and 23).

While trapping records indicate *P. alstoni* to be common in the region where Musser worked, he rarely saw the squirrels; they were quiet and wary compared with the *P. topapuensis* (see that account) he encountered. Occasionally squirrels were seen traveling through the upper canopy and sometimes dashing along tops of rotting treefalls on the ground in forested ridgetops, hillsides, and stream terraces. Calls heard were similar to those vocalizations of *P. topapuensis*. So too were the factors eliciting alarm calls: approaching rain, human sounds, and diurnal avian predators.

Contents of somachs indicate that soft fruits and insects comprise the diet (table 24). Remains of figs were the most common fruit found in stomachs. In addition to remains of fruit, several stomachs contained a variety of insects, most of which would be encountered in tree crowns (table 57). Macrolepidopteran larvae (caterpillars) feed on foliage and, judged by the large numbers in stomachs, were actively gleaned from leaf surfaces by the squirrels. Larvae of buprestid beetles live beneath the bark of standing trees and are dug out. Along with fruit, arboreal termitid termites were in two stomachs, one with about two dozen workers and soldiers, but the other packed with these insects. The squirrels had located and scratched open a nest adhering to a limb in the tree crown either before or after eating fruit. Adult beetles and beetle larvae other than buprestids, as well as the occasional ant are also picked off surfaces of leaves and bark. The few ant pupae found in stomachs were likely dug out of a nest.

ECTOPARASITES: The only record is the sucking louse *Hoplopleura alstoni*, n. sp. (table 56), that we describe in a following section; this species of louse is unique to its host.

SYMPATRY: The range of *P. alstoni* on the central core and southeastern peninsula of mainland Sulawesi overlaps distributions of *P. murinus*, *Rubrisciurus rubriventer*, and the ground squirrel, *Hyosciurus ileile* (table 6). In

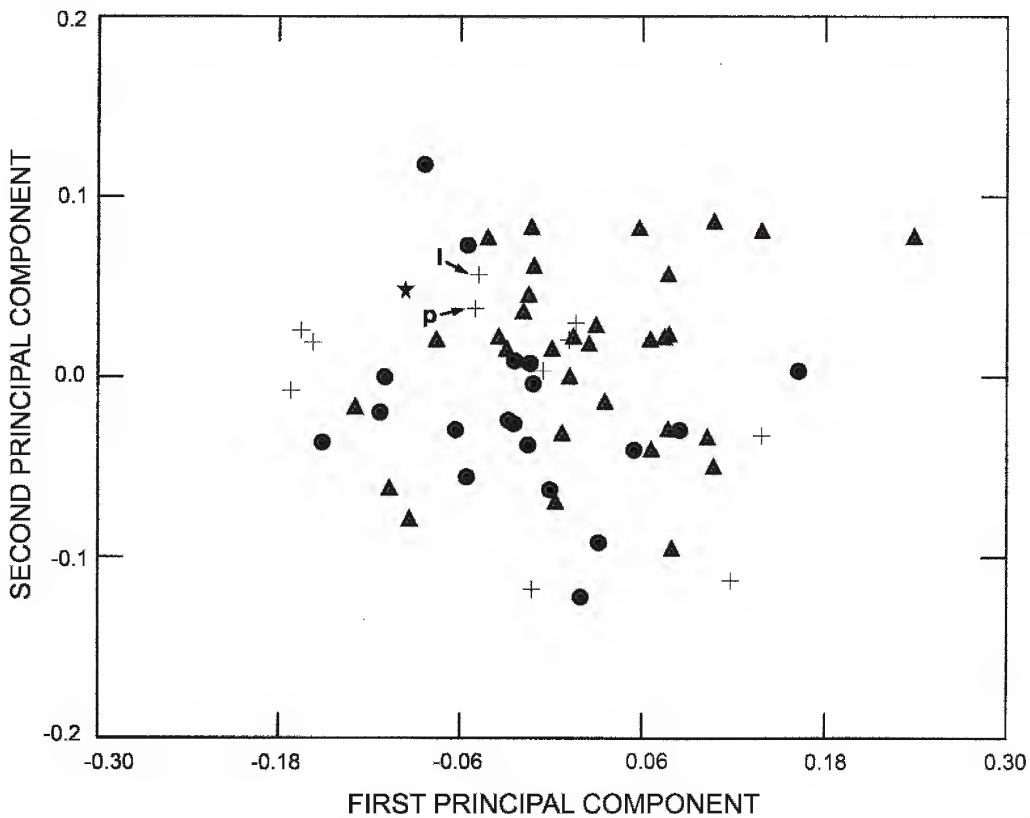

Fig. 21. Specimen scores representing population samples of *Prosciurillus alstoni* projected onto the first and second principal-components extracted from principal-components analysis. Symbols identifying samples are: filled circle = Pinedapa (N = 19); filled triangle = Kuala Navusu and Sungai Tolewonu (N = 32); cross = southeastern peninsula (Wawo, Masembo, Lalolei, Mowewe, Sungai Ahua; N = 11); star = Mapane, lectotype of *sarasinorum*. Abbreviations: l = lectotype of *mowewensis*; p = paralectotype of *mowewensis*. See table 23 for correlations and percent variance.

the lowlands behind Kuala Navusu and Sungai Tolewonu at the northern section of the central core of Sulawesi, Musser trapped *P. alstoni* in the same traplines where he encountered the other three species, and sometimes in the same traps (table 24).

SYNONYMS: Four scientific names represent samples of *P. alstoni*. Information covering their type specimens and reasons behind their allocations is summarized below.

Sciurus tonkeanus Meyer, 1896: 25, plate X, figure 4. LECTOTYPE: SNSD B3178 (skin mounted in a live pose, without a skull), an unsexed adult purchased from Charles Cursham in 1889. TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tengah, east-central peninsula of Sulawesi, Tonkean (near Sinorang), 01°24′S, 122°30′E, on the coastal plain, 0–100 m (locality 5 in gazetteer and on map in figure 11).

Feiler (1999: 407) identified SNSD B3178 as the "holotype" and eight additional specimens as "paratypes." Meyer (1896: 25) had before him an unspecified number of flat skins without skulls and postcranial skeletons ("platte Felle ohne Knochen") when he named and diagnosed *tonkeanus* and did not designate a holotype, the usual practice at the time. Feiler's indication therefore has made SNSD B3178 the lectotype of *Sciurus tonkeanus* Meyer, 1896, the other eight specimens being paralectotypes, designations in agreement with Article 74.5 in the Code (ICZN, 1999: 82–83): "In a lectotype designation made before 2000, either the term 'lectotype,' or an exact translation or equiv-

TABLE 23
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus alstoni*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 21.

Variable	PC1	PC2
ONL	0.013	0.002
CBL	0.018	0.005
ZB	0.019	−0.003
IB	0.021	−0.003
LN	0.030	0.023
LR	0.024	0.012
BR	0.042	−0.041
MB	0.005	−0.002
HBC	−0.005	0.004
LO	0.012	0.004
LD	0.036	0.018
LBP	0.015	−0.007
PPL	0.020	0.004
BBP	0.011	−0.010
LB	0.015	0.001
CLPMM	0.003	0.005
Eigenvalues	0.007	0.003
Percent variance	34.183	14.214

alent expression (e.g. 'the type'), must have been used or the author must have unambiguously selected a particular syntype to act as the unique name-bearing type of the taxon. ..." By using the term "holotype" (an "equivalent expression (e.g. 'the type')," Feiler has "unambiguously selected a particular syntype to act as the unique name-bearing type of the taxon."

The eight paralectotypes (SNSD 3179–86) are unsexed and without skulls. All are unstuffed pelts that "seem to have dried in the position they just happened to be in and were not prepared 'properly' ... the ears are all flat or broken and the tails bent or lost." (C. Stefen, in litt., 2008).

Clara Stefen kindly sent us color images of the lectotype and paralectotypes, and based upon them, along with Meyer's (1896) description and color plate (fig. 9), we can write that *tonkeanus* closely resembles the holotypes of *sarasinorum* (fig. 10) and *alstoni* (fig. 16) in coloration of the fur covering body and tail, differing only in color of the ears and expression of tufts (see appendix 3 for Meyer's description in the original German). The white covering on the medial surface of each ear that extends beyond the margin of the pinna to form a conspicuous white tuft that is so characteristic of most examples of *P. alstoni* is absent from the sample of *tonkeanus*. Instead, outer and inner surfaces of the ears are dark brown or buffy, and these hairs project slightly beyond the margin of the pinna to form a short and inconspicuous fringe in most specimens, and a short tuft in others. We don't know if color and size of the ear fringe seen in the sample from Tonkean are characteristic of populations inhabiting all forests on the east-central peninsula, for no other samples have been collected in that region. We do know that the *tonkeanus* ear pattern is present at a low frequency in our samples from the central core and southeastern peninsula (see discussion in the section covering geographic variation); these specimens closely resemble the condition in the lectotype and paralectotypes of *tonkeanus*, as shown in Meyer's plate (fig. 9) and the color images provided by Clara Stefen.

More samples of tree squirrels from the east-central arm of Sulawesi, especially in the region near the central core, are required to assess the actual range of variation in color and size of the ear tufting in those populations. Although we are currently ignorant of the variation in cranial and dental dimensions among populations on the east-central arm, we suspect the ranges of those dimensions would not be significantly different than those we have uncovered here for our samples from the central core and southeastern peninsula (table 19), but only through study of new material from the east-central peninsula can our assumption be tested. Until then we regard the sample of *tonkeanus* to represent a population of *Prosciurillus alstoni* in which the ears have buffy fringes and lack white ear tufts, at least in the type series, the only sample currently available for study.

Sciurus sarasinorum Meyer, 1898: 1 (1899: 21, pl. V). LECTOTYPE: SNSD B3826 (skin and skull; measurements are listed in table 14), an adult male collected during February 1895, by Fritz and Paul Sarasin. TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tengah (northern portion of the

Fig. 22. The habitat of *Prosciurillus alstoni* in tropical lowland evergreen rain forest on flat terrain near Musser's camp at Kuala Navusu, 30 m. The large tree is *Dracontomelon dao*, which emerges above the upper canopy layer, is scattered on flats and lower slopes of ridges, and is one of the largest trees in the forest. The tree photographed is about 150 ft high, 4 ft diameter just above the buttresses, and 10 ft across the bases of the buttresses. The tree squirrels *Rubrisciurus rubriventer* and *Prosciurillus murinus* were trapped in the same forest. Range of ambient temperatures recorded during the sampling period is listed in table 2. Photographed in 1975.

Fig. 23. Hillside forest near Kuala Navusu, 60 m. Aminudi is touching an *Artocarpus sericarpus*, one of the breadfruit species that is scattered through the forest on streamside terraces and lower margins of hillsides. The forest on hills tends to be shorter than the tall forest on the flats. The palm in the center of the photograph, *Licuala rumphii*, is common in the understory. Examples of *Prosciurillus alstoni*, *P. murinus*, and *Rubrisciurus rubriventer* were trapped here. Photographed in 1975.

central core), Mapane, 01°26′S, 120°40′E, near sea level at the southern margin of Teluk Tomini (locality 4 in gazetteer and on map in figure 11).

Clara Stefen sent us color photographs of the skin and skull of the specimen collected at Mapane—and we also have in front of us prints of the skull derived from negatives

TABLE 24

Summary of Habitat at Trapping Sites, Stomach Contents, and Other Relevant Information for Specimens of *Prosciurillus alstoni* Collected by Musser in Central Sulawesi, 1975–1976

Collection locality, specimen number, elevation, and month and year of collection are included. Descriptions of the trapping sites and contents of stomachs, slightly edited, are from Musser's field journals (in mammalogy archives at AMNH). The two collection localities (Kuala Navusu and Sungai Tolewonu) are in tropical lowland evergreen rain forest. All squirrels were caught during the day in Conibear traps (rats taken in the same traps were caught during the night). Unless noted differently, trapping sites were in primary forest formations.

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
Kuala Navusu 226076 (3080) 226079 (3105) 226080 (3170) 226081 (3265)	31	Aug. 1975	On trunk (diameter 5 in.) of tree that had fallen across stream, connecting the stream terrace on one side to the opposite bank and bordering forest, trunk 5 ft above surface of water; just up from camp. ASE 3105 caught during early morning in September 1975; ASE 3170 and ASE 3265 also caught during September. A *Prosciurillus murinus* was trapped on same spot on a different day. **Stomach of ASE 3080**: distended with freshly consumed mixture of pink and tan fruit pulp consisting mostly of fig seeds and rind; also a few small macrolepidopteran larvae. **Stomach of ASE 3170:** partially full of fruit pulp, along with fibrous material, probably the outside of a fibrous seed around which the pulp was removed.
226078 (3092)	31	Sept. 1975	On rotting trunk (1 ft diameter) lying on flat, wet ground on forested terrace below camp.
226077 (3093)	31	Sept. 1975	On rotting trunk (1.5 in. diameter) lying in rattan and shrub understory on wet bank of stream below camp. Caught during early morning.
226086 (3228)	40	Sept. 1975	On trunk (6 in. diameter) lying across main stream; trunk is at water level and usually inundated with every rise in stream after rains. **Stomach**: full of figs (mostly the tiny fig seeds) and a little bait.
226083 (3168)	40	Sept. 1975	On rotting section of trunk (8 in. diameter) lying across deep canyon containing tributary of Kuala Navusu. **Stomach**: full of brown fruit mash.
226084 (3276)	40	Sept. 1975	On rotting trunk (8 in. diameter) lying across steep tributary ravine. *Rubrisciurus rubriventer* was caught at the same spot on a different day. **Stomach**: full of fruit, some of it figs; also macrolepidopteran caterpillars.
226085 (3308)	40	Sept. 1975	On long, smooth trunk of *Livistona* palm that had fallen across part of stream terrace, connecting one terrace with that on the other side of the stream; trunk about 10 ft above water surface. A *Prosciurillus murinus* was trapped at same spot on a different day. **Stomach**: empty.
226087 (3584)	53	Nov. 1975	On trunk (6 in. diameter) lying across deep ravine dissecting forested hillsides where the trees *Artocarpus sericarpus* and *Myristica* sp. are common. **Stomach**: full of tan fruit mash.
226088 (3335) 226090 (3365) 226095 (3432)	122	Oct. 1975	On rotting trunk (5 in. diameter) lying across deep streambed (10 ft above rocky bed) and 4 ft above slope on either side of stream (now dry). Dense undergrowth and scrubby forest on either side of ravine. **Stomach of ASE 3365**: partially full of soft fruit mash; a few formicine worker ants, pupae of a larger ant species (probably dug out of a nest), several large beetle larvae, and macrolepidopteran caterpillars. **Stomach of ASE 3432**: partially full of soft fruit mash.

TABLE 24
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226089 (3367) 226091 (3375) 226092 (3397)	122	Oct. 1975	On trunk (10 in. diameter) lying horizontal in understory; from base of slope it extends 3 ft above ground and projects over deep (15 ft) rocky ravine where crown ends about 10 ft off ground on other side of ravine. Dense understory covering wet and rocky slopes. ASE 3397 caught in early morning. **Stomach of ASE 3367**: partially full of unidentifiable brown stuff and insects (several badly decomposed small caterpillars, remains of one large adult beetle, some buprestid beetle larvae, a heavily sclerotized beetle larva, and a few other larvae that are probably from a different kind of beetle.
226096 (3595) 226093 (3638)	122	Nov. 1975	On limb (6 in. diameter) bridging shallow, steep-sided ravine in good hillside forest adjacent to main stream in an area of recent tree-falls. **Stomach of 3595**: partially full of fruit mash.
226094 (3427)	122	Oct. 1975	On slender 40 ft trunk (5 in. diameter) of dead, small tree lying across ravine and enclosed stream; trunk extends from one side of ravine to the other side where it projects about 2 ft off the ground into dense and scrubby understory. The rat *Paruromys dominator* was caught in same place.
226097 (3366)	137	Oct. 1975	On trunk (8 in. diameter) leaning across hillside at 35° from ground into top of scrub in second-growth forest. **Stomach**: partially full of a little soft fruit mash, but mostly many beetle larvae of Buprestidae, some complete, others chewed into pieces—both large and small instars are represented.
226098 (3383) 226098 (3468)	137	Oct. 1975	On smooth trunk (8 in. diameter) lying across rocky slope in open understory near base of large, clifflike outcrop. Trunk lay 3 ft above ground for most of its length (60 ft). Trapped examples of *Prosciurillus murinus* on same spot during different days. **Stomach of ASE 3383**: full of reddish brown fruit mashed with a few macrolepidopteran caterpillar remains. **Stomach of ASE 3468:** full of tan fruit mash plus bright yellow fruit mash; also tiny white insect larvae that may have infested the fruit.
226100 (3656)	152	Nov. 1975	On large (60 ft long, 3 ft diameter) section of trunk lying on ground alongside shallow and wide part of main stream; good forest with broken canopy. **Stomach**: distended, half is bright yellow fruit mash that has been found in *Rubrisciurus rubriventer* and the rat *Taeromys celebensis*; the other half is pinkish-tan fruit mash mixed with sclerites and legs of a few small adult beetles.
226101 (3257)	229	Sept. 1975	On rotten trunk (6 in. diameter) lying across damp ravine that is well shaded by rattan and understory trees on steep slope above tributary stream. Caught *Prosciurillus murinus* at same spot on a different day. The rat *Maxomys hellwaldii* was taken on ground nearby.
Sungai Tolewonu 226510 (3855)	122	Jan. 1976	On rotting trunk (20 ft long, 6 in. diameter) lying across wet ravine in thick understory about 20 ft from edge of river. **Stomach**: full of brown fruit mash packed with worker and soldier termites (members of Termitidae). Squirrel clearly found the nest of arboreal termites. No other kinds of insects present.
226511 (3876)	122	Jan. 1976	On trunk lying across wet ravine 2 ft away from trunk where ASE 3855 was caught yesterday. Both of these tree trunks are wet and rotten, about the same size, and lay at 45° across the ravine near its confluence with river. Forest is short, understory is scrubby; tall canopy trees are Paba, Leutu, and others. **Stomach:** partially full of brown fruit mash; no insects.

TABLE 24
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226512 (3894)	122	Jan. 1976	On rotting branch (8 in. diameter, 15 ft long) that lay over depression on hillside just above river and below camp. In thick understory of shrubs, palm rosettes, saplings, and understory trees; Paba and Uru common canopy trees. **Stomach**: empty except for a few remains of undigested insects, mostly small fragments of sclerites.
226513 (3889)	152	Jan. 1976	On decaying trunk lying across tributary stream about 4 ft above water surface, bridging the two banks; caught early in morning. **Stomach**; full of brownish red fruit mash, rubbery pink mash; also containing numerous remains of macrolepidopteran caterpillars.
226514 (4151) 226515 (4228)	165	Feb. 1976	On large trunk of canopy tree that has fallen across main river between confluences of second and third long tributaries. Tree rests from river terrace across to rocky hillsides, is about 45 ft long and 1.5 ft in diameter, and rests 5 ft above water level. Trunk is free of vegetation except for a limb growing parallel to the trunk along its entire length, which has sprouted leaves and provides partial cover for the entire length of trunk. Caught ASE 4151 early in morning. The tree squirrels, *Prosciurillus murinus* and *Rubrisciurus rubriventer*, and rat, *Maxomys hellwaldii*, were taken on same spot. **Stomach of ASE 4151**: full of brown mash in which are mixed about two dozen termitid termites and remains of at least one small beetle.
226516 (4152)	198	Feb. 1976	On a slim (3 in. diameter) rotting trunk that lay across the left-hand fork of third large tributary; trunk extends from steep hillside bank across to stream terrace, 6 to 3 ft above water; caught early in morning. **Stomach**: nearly empty: brown mash, similar to that found in ASE 4151, pieces of insect legs.
226517 (4153)	198	Feb. 1976	On horizontal smooth trunk (3 in. diameter) of common understory *Eugenia* that is growing across the stream bed about 10 ft upstream from where ASE 4152 was caught; good forest, steep hillside on one bank, terrace on the other. **Stomach**: empty.
226518 (3928)	244	Jan. 1976	On decaying trunk lying across ravine of tributary stream far back and up from confluence with main river; intact hill forest, thick understory. **Stomach**: empty.
226519 (4053)	290	Jan. 1976	On a smooth trunk (10 in. diameter) 5 ft above water surface. This is one of several trees that have fallen; two other trunks extend from one side to other across top of ravine. Next to stream the forest understory is dense and scrubby; usual broken high canopy in back of ravine edge; caught early this morning. **Stomach**: nearly empty, bits of fig, mostly numerous pieces of small adult insects (sclerites, legs, antennae, some are from beetles).
226520 (4018)	305	Jan. 1976	On decaying trunk lying across branch of tributary stream in hilly headwaters that are covered with good hillside forest; tall broken canopy, dense tree understory and good ground cover. **Stomach**: empty.
226521 (4036)	305	Jan. 1976	On long, slender, moss-covered trunk (8 in. diameter, 40 ft long) that rests along one side of ravine, curves across onto other side; good hillside forest and near where the other squirrel, ASE 4018, was trapped yesterday; caught this morning. **Stomach**: partially full of remains of figs (rind with large seeds on stalks).

TABLE 24
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226522 (4038)	320	Jan. 1976	On smooth wet trunk (5 in. diameter) lying across a deep ravine (about 20 ft) that is a branch of the tributary in the very steep headwaters area. The remains of an old tree-fall lay over the ravine in this spot and the ravine margins are open and bare with the forest back from the ravine edges. **Stomach**: full of mostly a pinkish tan and spongy fruit mash, pieces of buprestid beetle larvae, and a few macrolepidopteran caterpillars.
226523 (3955)	335	Jan. 1976	On dead *Calophyllum* trunk (6 in. diameter, 30 ft long) lying across two channels of tributary stream in area where headwaters begin. Trunk is 3 ft off ground; several other trunks, all probably part of same old decaying tree-fall, are resting in scrubby understory. A huge emergent *Ficus* shades the area. **Stomach**: distended with pinkish tan fruit mash containing remains of figs and another kind of fruit; no insect remains.
226525 (4058)	335	Jan. 1976	On moss-covered decaying limb (8 in. diameter, 30 ft long) resting across branch of tributary in headwaters area. Good hillside forest on steep slopes; scattered tall trees form an open, high canopy; understory dense, forming closed canopy; undergrowth thick, especially along banks of ravine, providing good shade; area is cool and wet. Sun ferns, palm rosettes and adults, euphorbs, and figs are common components of understory. *Pometia pinnata* is common emergent, as is *Pterospermum celebicum*, *Elmerillia ovalis*, and other tall trees. The ground squirrel, *Hyosciurus ileile*, and rat, *Taeromys celebensis*, were taken at same spot.
226524 (4054)	366	Jan. 1976	On trunk of understory *Ficus* about 5 in. diameter that grows from side of ravine, up, and then over; so trunk is horizontal above ravine and stops halfway—meeting it is a slender 2 in. branch from a shrubby understory tree growing from opposite side of ravine. Very steep rocky slopes, the upper headwaters of tributary. Here the ravine is shallow and wide and consists of mostly washed slopes, now with trickling water. Forest on slopes above these ravines is short, dense, and not far from ridge top. This is highest spot we have seen *P. alstoni*; no sign of any other kind of squirrel in the *P. leucomus* group. **Stomach**: full of mostly tan fruit mash with tiny seeds—looks like fig; tiny legs and fragments of sclerites from a few insects.

made by G.H.H. Tate in 1951 during his visits to European museums. An unstuffed pelt dried in a distorted shape forms the skin. All appendages (ears, feet, and tail) are intact, and color of the fur is similar to that depicted in Meyer's color plate (1899; reproduced in fig. 10); the white ear tufts are conspicuous. The color hues of the pelt have retained the vibrant integrity of the live squirrel, even after 113 years. In color of upperparts, underparts, tail, ears, and extent of white ear tufts, the skin of SNSD B3826 is inseparable from H.C. Raven's sample collected in the 1920s from Pinedapa, southeast of Mapane, Musser's specimens collected in the 1970s from the Malakosa region northwest of Mapane (see map in fig. 17) and from G. Heinrich's samples collected in the 1930s from the southeastern peninsula. Except that the hues are paler in Anderson's (1879) color plate of "*Sciurus alstoni*" (see fig. 16), in particular the underside being much less brightly colored, that portrait bears a striking resemblance to the squirrels from Mapane

and Usu portrayed as *sarasinorum* in Meyer's color plate (see fig. 10), a population identity reinforced by their shared white and prominent ear tufts.

The skull of SNSD B3826 is intact except for a slight separation between the interparietal and occipital region, and a hole in the bony palate and one on top of the skull behind the nasals, which traces the path of a shotgun pellet. The left dentary is whole but the posterior ramus of the right dentary is in fragments, the anterior portion undamaged. Values from cranial and dental dimensions of the holotype fall within the range of variation of our samples that share similar fur coloration and patterning. In the ordination of specimen scores for population samples (identified in table 1) from the Malakosa region, Pinedapa, and the southeastern peninsula projected onto the first and second principal components extracted from principal-components analysis, the score for the holotype of *sarasinorum* clusters with scores representing specimens from those three geographic regions (fig. 21).

Meyer (1898: 1) based his description of *sarasinorum* on two specimens collected by the Sarasins and, as was the custom then, did not designate either as the holotype. One was collected at Usu ("Oesoe" on old maps; also spelled "Ussu"), 02°36′S, 121°06′E, near sea level at the northern end of Teluk Bone on February 18, 1896; the other was obtained farther north at Mapane on the south coast of Teluk Tomini in February 1895. Both specimens are represented by live poses in Meyer's (1899, pl. 5) color plate (reproduced here in fig. 10). Meyer (1899: 21) noted that the bottom pose represents the individual from Usu and was rendered natural size, while the top pose, which is one-half natural size, was drawn from the animal collected at Mapane. Both individuals have prominent white ear tufts, and are closely similar in color and patterning of the fur over body and tail.

Identifying the type locality and type specimen for *sarasinorum* is puzzling for anyone checking the published literature up to the late 1990s. Ellerman's (1940: 375) classic compendium on families and genera of living rodents noted only "Central Celebes" as the source of the two specimens. More than a decade later, in their checklist of land mammals of New Guinea, Celebes, and adjacent islands, Laurie and Hill (1954: 93) simply referred to both locations in their indication of a type locality: "Ussu, northern end of Gulf of Boni, and Mapane, southern end of Gulf of Tomini, Celebes." By the early 1990s, Corbet and Hill (1992: 304) had stated the type locality to be "Ussu, N end of Gulf of Boni, Sulawesi," which would imply that they regarded the specimen from Usu to be the type.

Neither Usu nor the specimen collected there in 1896 were listed in Feiler's (1999: 407) accounts of type specimens housed in the collection of the Staatliches Museum für Tierkunde at Dresden. He identified as "holotype" the specimen from Mapane, and that place as the type locality. No reference was made to a specimen from Usu. Perplexed, we inquired of Clara Stefen if the squirrel from Usu was still in the collection at Dresden, and she (in litt., 2008) wrote "I can't find any hint of it; it's not in the collection, but [I] did not even see an entry on the relevant systematic index card which seems odd to me, as they [the cards] probably were started under the directorship of Meyer."

We subsequently located the squirrel from Usu in the collection at the Naturhistorisches Museum Basel. In the mammalogy archives at AMNH we found a photograph of a skull from Usu taken by George H.H. Tate when he visited Basel in 1951. Our contact at Basel, Loïc Costeur, informed us that the specimen is listed in the museum's database; he subsequently found it in the collection, and sent us color images of the skin and skull. The adult skin (NMB 1199), prepared as a stuffed museum study specimen, is intact except for the head where large patches of skin are missing on the right and left side. The animal was clearly shot in the head and this damage is reflected in the skull (NMB 8080). The anterior half is intact and all teeth are present but all that remains of the posterior half is the roof of the braincase and cracked basicranial region still retaining the auditory bullae; the mandible is complete. The specimen was collected by Fritz and Paul Sarasin, and is one of the two studied by Meyer (1898, 1899). The specimen from

Mapane, which Feiler identified as the "holotype," has by that action become the lectotype of *Sciurus sarasinorum* Meyer, 1898 (see Article 74.5 in ICZN, 1999: 82–83), the specimen from Usu being the paralectotype. The two specimens, although from widely separate localities, are closely similar in body size and coloration of fur. They in turn are inseparable from our samples collected in the Malakosa region, Pinedapa, and the southeastern peninsula.

Sciurus mowewensis Roux, 1910: 519. LECTOTYPE: NMB 1626 (skin) and 4243 (skull), an adult female collected on February 23, 1903, by Fritz and Paul Sarasin. Measurements are listed in table 14. TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tenggara (southeastern peninsula of Sulawesi), Mowewe, 04°10′S, 121°52′E, approximately 500 m (locality 8 in gazetteer and on map in figure 11).

Roux based his description of *mowewensis* on an adult female (NMB 1626/4243) from Mowewe and an adult male (NMB 1627/4244) from nearby "Ahua River [= Sungai Ahua]," and compared them most closely with *sarasinorum*, known at the time only from the two specimens described by Meyer (1898, 1899). Roux's description (translated from the original in German; the German text is reproduced in appendix 5):

> The only species from the southeastern peninsula heretofore known has already been spoken of above [the previous description covered "*Sciurus sarasinorum*"]. In the new Sarasinian material there were two skins from two neighboring localities from about the central part of this region. These skins are very closely related to *Sciurus sarasinorum* though slightly different. The body size is the same as is that of the tail; the head is somewhat shorter.
>
> The two skins exhibit the same colouration. The hairs of the back are yellowish brown with black annulations; the brown colour is darker in the median zone than it is on the sides where it has a more grayish tone. I have observed the same in *Sciurus leucomus*. The tufts on the ears are very well developed; they are white with a distinct yellowish tint. The inside of the ears is equipped with fine fox red hairs. A yellowish brown ring of fine short hairs surrounds the eyes. The sides of the snout to almost under the eyes are brick red. In *Sciurus sarasinorum* these parts are of the same colour as the rest of the head. The surface of the belly, the underside of the limbs and a stripe in the anal region reaching to the first fifth of the tail are brick red. On the upper sides of the feet this coloration is somewhat lighter and mixed with black. The tail displays about the same colouring as that of *Sciurus sarasinorum*; it is not on the whole, however, as black, but is more brown because the brown rings are broader The subterminal portion of the hair is white; the hairs on the tuft are also mostly tipped whitish. [Roux listed measurements for the two specimens; see appendix 5]
>
> It is most likely that the southern peninsula also harbours species of *Sciurus* that belong to the *Leucomus* group. So far, however, they are not known.

Roux basically redescribed *sarasinorum*, which was detected by Moore (1958: 2): "Inspection of the Archbold material [at AMNH], Roux's (1910, p. 519) description, and Meyer's (1899, p. 5) colored plate of *sarasinorum* shows that Roux's squirrel is an obvious synonym of *sarasinorum*." This attribution is reinforced by our inspection of the color images of the lectotype and paralectotype (these designations were made by someone at Basel and entered into their unpublished catalog of type specimens, according to Loïc Costeur, who examined the specimens for us; Roux had not identified either specimen as the holotype) sent to us by Loïc Costeur. Following this manuscript catalog, we hereby formally designate NMB 1626/4243 the lectotype of *Sciurus mowewensis* Roux, 1910, the other specimen (NMB 1627/4244) being the paralectotype. Each skin is prepared as a dry and stretched pelt; color of the fur is still bright and unaltered. The pattern of color on the body and tail, along with their prominent white ear tufts, identifies the specimens as *sarasinorum*, and in turn as examples of the older name, *alstoni*, and not something uniquely distinct.

Values for cranial and dental dimensions measured fall within the range of variation for our samples of *P. alstoni* from the Malakosa region, Pinedapa, and the southeastern peninsula (table 19). Except for missing second molars and a missing third premolar from the holotype, both skulls are intact, as can be seen from the photographs taken by G.H.H. Tate in 1951 (stored in the

mammalogy archives at AMNH). Loïc Costeur measured both skulls for us. His values, along with those from the holotype of *sarasinorum* and our samples from central Sulawesi and the southwestern arm, became the subjects of principal-components analysis, which resulted in the ordination depicted in figure 21. The scores for the types of *mowewensis* cluster with points representing specimens from Pinedapa and the Malakosa region; the score for the holotype of *sarasinorum* is nearby. Scores denoting the AMNH specimens from the southeastern peninsula are scattered throughout the cluster derived from the samples from the Malakosa region and Pinedapa. There is no evidence from cranial and dental dimensions or proportions derived from the two skulls of *mowewensis* indicating they are anything other than another sample of *sarasinorum*, which identifies a population for which *P. alstoni* is the oldest name.

Sciurus elbertae Schwarz, 1911: 639. HOLOTYPE: SMF 721 (a skin and skull were described by Schwarz; the skull is present in the Senckenberg Museum but the skin is missing [G. Storch, in litt., 2008]; measurements are listed in table 14), an unsexed adult collected by J. Elbert (original number 227). TYPE LOCALITY: Indonesia, Propinsi Sulawesi Tenggara (southeastern peninsula and offshore islands of Sulawesi), Eempuhu, Pulau Kabaena (05°15′S, 121°55′E), off the coast of the southeast peninsula (see map in figure 11). Schwarz identified the type locality as "Eempuhu, East Kabaëna." No elevation is attached to the specimen. Highlands constitute most of the island with topographic relief ranging from sea level to 1570 m.

Schwarz (1911: 639) examined two specimens, each consisting of a skin and skull, and regarded them to be "A pale-coloured member of the *Sciurus leucomus*-group." Judged from his description, the fur of *elbertae* is somewhat paler than the rich and darker hues typical of *sarasinorum* from the mainland. No reference to ear tufts were made, only that the general color of the upperparts was brownish (between "olive" and "raw umber") "with a creamy-buff tinge on head." We have not seen a "creamy-buff tinge" on the head of any specimen of *P. alstoni*, or any other specimen in the *P. leucomus* group. Unfortunately, both skins are missing from the collection at Senckenberg so we cannot determine if Schwarz was actually describing "creamy-buff" ear tufts, which would make sense. Both specimens from adjacent Pulau Buton have whitish buff ear tufts (see discussion of geographic variation).

The skull of the holotype (SMF 721) is complete except for broken basicranial and occipital regions; all premolars and molars are fully erupted and show moderate wear. The skull of the paratype (SMF 4878), slightly damaged, is that of a juvenile (G. Storch, in litt., 2008). Values for the cranial and dental dimensions that could be measured (by G. Storch) are listed in table 14. Some dimensions are smaller in the skull of *elbertae* compared with samples of species in the *P. leucomus* group (contrast tables 13 and 19); values for interorbital breadth, and lengths of nasals, rostrum, diastema, and bony palate, for example, are less than the range of values for these variables in the sample of *P. alstoni*. Length of PM4–M3 (7.3 mm) is within the range of variation for most of our samples of the *P. leucomus* group, which suggests to us that although all teeth are erupted and moderately worn, the skull of SMF 721 may be from a very young adult. Currently, we cannot assess the significance of the mensural differences described here without a larger sample from Pulau Kabaena containing a range of ages, from very young to old adults.

Schwarz compared *elbertae* with the skull of what he identified as "*Sciurus mowewensis*" collected on Pulau Buton. Among the distinctions he noted (primarily some smaller dimensions of *elbertae*) was the presence of a distinct medial spine extending from the posterior margin of the bony palate in *elbertae* and its absence in the Buton specimen. Among our samples of *P. alstoni* (of which *mowewensis* is a synonym), the posterior margin of the bony palate exhibits three variants: a straight edge, a margin interrupted by a median bony nubbin, or "a distinct median spine" marking the edge.

On our copy of the published description where Schwarz indicated *elbertae* to be a member of the "*Sciurus leucomus*-group,"

G.H.H. Tate had crossed out "*leucomus*" and scribbled "*nigrovittatus* or *notatus*" in the margin. We had also considered these possible identifications but rejected them. Ranges of both species cover primarily peninsular Thailand and Malaya, and islands on the Sunda Shelf. *Callosciurus nigrovittatus* is recorded from peninsular Thailand, the Malay Peninsula, Sumatra and Java, and the small islands of Tioman and Saddle on the Sunda Shelf (Corbet and Hill, 1992: 292). This squirrel is larger-bodied than Schwarz's *elbertae*. Schwarz, for example, recorded length of the "upper tooth row" (PM3–M3) as 7.9 mm, which is well outside the observed range of values (minimum, 8.3–9.2 mm; maximum, 9.0–9.7 mm; $N = 93$) given by Sody (1949: 95) for 17 samples from Java, the island supporting populations of *C. nigrovittatus* closest to Sulawesi. *Callosciurus nigrovitattus* has gray underparts and prominent white and buffy parallel stripes on sides of the body (see color pl. 7 in Medway, 1969, and pl. III in Askins, 1988), ventral coloration and body patterning unlike *elbertae* or any other kind of squirrel known from Sulawesi.

Callosciurus notatus has a broader geographic range than *C. nigrovitattus*, and is found on peninsular Thailand and Malaya; the larger Sundanese islands of Sumatra, Java, and Borneo; many smaller islands on the Sunda Shelf; east to Pulau Lombok in the Lesser Sunda Islands; and on Pulau Salayar, just south of the southwestern peninsula of Sulawesi (Corbet and Hill, 1992: 291). Sody (1949: 82) published observed ranges for length of upper tooth row derived from 17 samples of *C. notatus* from Java (minimum, 8.4–9.6; maximum, 8.6–10.3 mm; $N = 92$) and for five specimens from Pulau Salayar, off the southern coast of Sulawesi's southwestern peninsula (minimum, 9.3 mm; maximum, 9.7 mm), illustrating a range much greater than the value of 7.9 mm for the holotype of *elbertae*. *Callosciurus notatus* resembles *C. nigrovitattus* in having parallel buffy and white stripes on each side of the body; the populations on Java have either gray or buffy underparts and specimens from Pulau Salayar have dull buffy venters (see the color plates in Medway, 1969, and Askins, 1988; pl. 25 in Payne et al., 1985; Corbet and Hill, 1991: 292). The two examples of *elbertae* are not examples of either *C. nigovitattus* or *C. notatus*.

Prosciurillus weberi (Jentink, 1890)

Sciurus weberi Jentink, 1890: 115, pl. VIII, pl. X figs. 1–3.

Lectotype and Type Locality: The lectotype of *Prosciurillus weberi* is an adult female (RMNH 13342) collected by Max Weber in February of 1889. A mounted skin and accompanying skeleton comprise the specimen. The skull is intact. Measurements are listed in table 13. Jentink (1890: 115) had "three adult *skins*, two *skeletons* and one *skull*" at hand when he described *weberi*, and with the aid of Chris Smeenk at Leiden, Wim Bergmans at Amsterdam, and Paula Jenkins at London, we have located all the elements that are the basis for Jentink's description. Only RMNH 13342 remains at Leiden, and following Chris Smeenk's suggestion (in litt., 2008), we select it as lectotype, following Article 74.1 of the Code (ICZN, 1999: 82). One of Weber's specimens is now in the collection at the Natural History Museum in London (BMNH 94.7.4.6, a skin only), which becomes a paralectotype. Two of Weber's other specimens are in the collection at the Zoological Museum, Amsterdam: ZMA 11.327, a mounted skeleton (including skull) and ZMA 11.328, a mounted skin and skull; both are paralectotypes. (Chris Smeenk wrote us that in 2010, the Amsterdam collections will be moved to Leiden and become incorporated into the Leiden collections; the catalogue numbers will remain unchanged and preceeded by ZMA.)

The type locality is Palopo ("near Palopo" is indicated on some tags), 03°01′S/120°13′E, 0–100 m (locality 2 in the gazetteer and figure 11) in the southern lowlands of the central core of Sulawesi, Propinsi Sulawesi Selatan, Indonesia. Jentink (1890: 115) gave "Luwu near Palopo, central Celebes" as the type locality; Luwu is the administrative district containing Palopo.

Emended Diagnosis: As in most of the other members of the *Prosciurillus leucomus* group, *P. weberi* has a moderate-size body and a tail equal to or shorter than length of the head and body. It contrasts with the other

four species by the following combination of pelage traits (see table 12): **(1)** dorsomedial surface of each ear covered with long black hairs projecting beyond ear rim to form a prominent tuft; **(2)** no bright ochraceous hairs lining inside of the pinnae, which is the same color as the fur on neck and head; **(3)** no nape patches behind the ears; **(4)** prominent middorsal black stripe extending along back from neck to base of tail **(5)** reddish orange underparts; and **(6)** currently known only from lowlands fringing the northwestern margin of Teluk Bone.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: Records of *P. weberi* are represented only by the voucher specimens collected between 1889 and 1940 near Masamba and Palopo in lowlands fringing the central mountains to the west and Teluk Bone to the east in the southeastern margin of Sulawesi's central core (see gazetteer and map in figure 11). These sites are no higher than 100 m.

The known range of *P. weberi* is allopatric to those of two other members in the *P. leucomus* group. To the east, *P. alstoni* occurs primarily in lowland forest habitats in the eastern portion of the central core, the east-central peninsula, the southeastern peninsula, and has been collected from two islands (see map in fig. 11). Usu, in the coastal lowlands fringing the southwestern end of Teluk Bone, is the collection locality for *P. alstoni* closest to Masamba, which is about 80 km to the west of Usu. See the account of *P. alstoni* for an expanded discussion contrasting the geographic ranges of the two species.

Prosciurillus topapuensis inhabits forests in the mountains to the west of Masamba and Palopo (see map in fig. 11). No specimens have been collected lower than 350 m and no collection localities are close to the range of *P. weberi.* Surveys in the foothills west of Masamba and Palopo, provided that intact forest is present, are required to determine the distributional relationships between the two species. Here *P. weberi* may be restricted to lowland tropical evergreen rain forest and *P. topapuensis* to montane forest habitats.

The actual geographic distribution of *P. weberi* is unknown. If it is restricted to tropical lowland rain-forest habitats, the species may occur all along the eastern coast of the central core, westward through the northern part of the Tempe Depression along the margin of the mountains, and north along the western coast possibly to the Palu area—the range would fringe the west-central foothill and mountain distribution of *P. topapuensis.* No samples of squirrels are available from these lowlands and no place along those coasts or in the Tempe Depression has been carefully surveyed for small mammals. Much of the southern part of this lowland fringe has been deforested (see maps in Whitten et al., 1987: 102, and Supriatna et al., 1992: 37), so we may never know what member of the *P. leucomus* group inhabited the orginal forest cover.

In the past, *P. weberi* may have ranged across the Tempe Depression south throughout lowlands of the southern part of the southwestern peninsula. No modern specimens of the *P. leucomus* group have been collected in that region, but at least one once occurred there. A subfossil mandibular fragment collected from a cave in the Maros region attests to the former presence of a tree squirrel, possibly representing *P. weberi* (see the account of *Prosciurillus* sp.). Tree squirrels may still exist in the small patches of lowland forest remaining on the southern part of the peninsula, but most of the region is densely populated agricultural land (see the maps in Whitten et al., 1987: 102, and Supriatna et al., 1992: 37).

Our experience with nonvolant endemic Sulawesi mammal distributions indicates that the range of *P. weberi* is unusual. As currently documented by voucher specimens, its range is not congruent with any other endemic mammal, a pattern contrasting with many of the distributions shared by species in other mammal groups. This discordance suggests to us that either the range of *P. weberi* will prove to be greater than what is now represented by specimens (as we outlined above) or that it once occurred on the southwestern peninsula but is now extinct (and possibly represented by the subfossil from the Maros region).

A young adult *Prosciurillus weberi* in MZB (6255) bears a skin tag indicating it was collected in 1908 from "Menado" (see also Sody, 1949: 107), but was certainly mislabeled. *Prosciurillus leucomus* is the only

member of the *P. leucomus* group that has ever been collected from the Manado region (see gazetteer for *P. leucomus*).

DESCRIPTION: "This beautiful Squirrel," wrote Jentink (1890: 115–116) of *weberi*,

> belongs to a group of middle sized species, consisting of *Sciurus leucomus*, *rosenbergii* and others having no stripes or bands on the sides of the body and more or less prominently pencilled ears. It is distinguished from all the hitherto known East-Indian-Squirrels by having a rather *broad black band along the spine of the back*, running from the neck, increasing in broadness in the middle of the back and diminishing towards the root of the tail. The ears are adorned with rather long black hairs which form a kind of small pencil. It is to be observed that in one of the three type-specimens the black earpencils are slightly tipped with white. For the rest the upperparts and sides of the head and body and the legs are covered with very soft hairs showing a reddish-black tinge, occasioned by being each black hair ringed with reddish; the underside of head, the breast, belly and inside of legs have the black hairs largely tipped with red, so that the named parts present a fine red hue. The tail shows undistinct rings; upperpart of tail with hairs ringed with red and black ending in white tips; towards the tip of the tail the red and white disappear so that the tip of that organ is black; as the tail is distichous it is evident, that on the underside the red tinge prevails. The whiskers are black; they reach as far backwards as the end of the earpencils.

In its physical size and proportions of feet and tail, *P. weberi* closely resembles *P. alstoni* (table 15). Dark brown upperparts sprinkled with orange and black, along with dark reddish or reddish orange underparts, are also common to both species. The combination of prominent black ear tufts and black middorsal stripe, however, is unique to *P. weberi*, and is illustrated in Jentink's (1890) color plate of *weberi* posed on a tree limb. Views of the skull are also provided by Jentink. Number and position of teats match the pattern seen in all members of the *P. leucomus* group (one postaxillary pair, two inguinal pairs). Conformation of the skull is closely similar to that illustrated for *P. alstoni* and *P. topapuensis* (figs. 12–14); cranial and dental measurements are summarized in table 17. See the account of *P. alstoni* for additional information.

COMPARISONS: *Prosciurillus weberi* is allopatric to the geographic ranges of *P. alstoni* and *P. topapuensis* and requires close comparisons with those species. Contrasts are described in those two accounts.

GEOGRAPHIC VARIATION: Because the few specimens of *P. weberi* are from the same small geographic area, we cannot assess the nature of geographic variation in this species.

ECOLOGY: Other than knowing that the collection localities were in lowland tropical evergreen rain forest, we have no other information about the biology of *P. weberi*. We suspect that its habits are similar to those of *P. topapuensis* and *P. alstoni*, which inhabit the upper canopy and eat mostly soft fruits, seeds, and insects.

ECTOPARASITES: No records.

SYMPATRY: Only *Rubrisciurus rubriventer* has been collected at the same place as *P. weberi* (see gazetteer and table 6), but *P. murinus* probably inhabited the same forests at the time the specimens of *R. rubriventer* and *P. weberi* were collected.

SYNONYMS: None.

Prosciurillus topapuensis (Roux, 1910)

Sciurus topapuensis Roux, 1910: 518.
Callosciurus leucomus hirsutus Hayman, 1945: 576.

HOLOTYPE AND TYPE LOCALITY: The holotype of *Prosciurillus topapuensis* is an adult female (NMB 1628/4245) collected by Paul and Fritz Sarasin on September 16, 1902. A dry skin and accompanying skull comprise the holotype. The skin is an intact flat pelt. Most of the skull is present; the right zygomatic arch, most of the basioccipital and the occipital condyles are missing, as are the left third and fourth premolars and third molar. The mandible is complete except for missing coronoid processes, and all teeth are missing from the right dentary. Measurements are listed in table 13.

The type locality is Gunung Topapu (approximately 02°S, 120°15′E; estimated from a copy of the original map used by Paul and Fritz Sarasin), 1550 m (locality 16 in gazetteer and map in figure 11). This highland is contained in the mountains west of Teleboi in the Bada region of the west-central region of Sulawesi, the north and

western portion of Propinsi Sulawesi Selatan, Indonesia.

Our identification of the holotype of *topapuensis* as an example of the *P. leucomus* group requires explanation. A single specimen is the basis of Roux's (1910: 518) description of *Sciurus topapuensis* and his account is short (translated from the original in German; the German text is reproduced in appendix 5):

> This animal most closely resembles *Sciurus tonkeanus* Meyer but displays certain differences. The general colouring of the head, the back and the tail is the same, the ventral side being different. Instead of the common brick red colour these have a grayish Yellow tinge, the base of the hairs being grey while the tips are more yellowish.
>
> The ears are quite distinctly tufted, the tufts being of the same colour as the head. The yellowish tone is somewhat brighter on the sides of the body and on the limbs than it is on the back. The tail hairs have three broad yellowish brown rings of which the two basal ones are slightly darker coloured than the third subterminal. Most of the hairs of the tail tuft are black with a broad yellow terminal ring.
>
> Measurements: Total length, 30; head length, 5; body 10 cm; tail with tuft, 15, tuft, 5.5 cm; hind foot c.u., 4.1; front foot c.u., 2.5; ear with tuft, 1.3 cm.
>
> To judge from the skull the animal is fullgrown. There is no difference between this skull and that of *Sciurus leucomus*. The dimensions of this form are somewhat under normal for the species of the *Leucomus* group. Furthermore, the ventral side is brick red in all the other species. Only in this species is it grey. I am not able to determine whether this is ascribable to seasonal variation or not.

Roux compared the skin with "*Sciurus tonkeanus*" [= *Prosciurillus alstoni*], noting close resemblance between the two in color of the fur over the head, back, and tail, but a sharp difference in coloration of the underparts. Instead of being "brick red" as in *tonkeanus*, the venter was described as grayish yellow, the base of the hairs being gray and the tips yellow. Later in the account, Roux referred to the underparts as gray. He also noted the presence of distinct ear tufts the same color as the head, and that the yellowish tone seen on the back was brighter along sides of the body and on the limbs.

Roux's references to "yellow" ("gelb") and "yellowish" ("gelblich") actually refer to slightly different buffy tones. On all specimens we assign to *P. topapuensis* (see gazetteer), the dorsal fur is a rich brown with buff highlights intermixed with black, a reflection of the black and orange or buff banding on the overhairs. Sides of the body and dorsal surfaces of the limbs are slightly paler (grayer) because the buffy bands of the hairs are much paler than those on the back, ranging from pale buff to cream. The coat covering underparts of these specimens is dark gray speckled or washed with pale buff or cream—the hairs are gray for most of their lengths and tipped with pale buff or cream, a combination reflecting Roux's "yellowish buff." Overall, the underparts appear dark gray flecked with buff, as Roux noted (a few specimens have dark gray underparts tinted with silver—a dark grayish white), and contrast sharply with the reddish venters common to all the other species in the *P. leucomus* group. Most specimens we examined exhibit black ear tufts ranging in expression from prominent to less conspicuous; a few individuals sprout tufts containing fewer black hairs with the result that the ears appear nearly inseparable from color of the head, the pattern Roux described for the single specimen of *topapuensis* he examined.

Coloration of the fur on the skin of the holotype of *topapuensis* has altered through the years in storage. Loïc Costeur kindly sent us a color image of the skin, which is preserved flat, unstuffed. The black bands on hairs of the back are now dark brown, the buffy bands yellow (the color of straw); the remnants of the underparts are paler than upperparts but yellowish with only a hint of the original gray.

Although the skull of the holotype is damaged, Loïc Costeur was able to measure all but four of the cranial and dental dimensions we investigated (table 26) and the values were included in our multivariate analyses. In the ordination showing specimen scores projected onto first and second principal components in figure 26, the score representing the holotype of *topapuensis* clusters with those for specimens from Sungai Miu and Sungai Sadaunta; falling nearby are

the scores representing specimens from Gunung Kanino, Besoa, and Rano Rano.

EMENDED DIAGNOSIS: *Prosciurillus topapuensis* shares with other members of the *P. leucomus* group a body moderate in size (tables 15, 16), but contrasts with the other four species by the following combination of pelage traits (see table 12): **(1)** tail averages shorter relative to length of head and body; **(2)** dorsomedial surface of each ear covered with long black hairs projecting beyond ear rim to form a conspicuous black tuft on most specimens; **(3)** no bright ochraceous hairs lining inside of the pinnae, which is the same color as the fur on neck and head; **(4)** no nape patches behind the ears; **(5)** no middorsal black stripe extending along the back from neck to base of tail **(6)** fur over upperparts thicker and subdued in tone on squirrels from high altitudes; **(7)** dark gray underparts lightly brushed with silver, pale buff, or ochraceous tones; and **(8)** a geographic range restricted to the western mountainous portion of Sulawesi's central core, where the species ranges in altitude from tropical lowland evergreen rain forests covering foothills to montane rain-forest formations.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: Voucher specimens identified as *P. topapuensis* describe a range concordant with valleys, foothills and mountains covering the western portion of the central core of Sulawesi, from Danau Lindu and surrounding highlands in the north (about 01°19′S, 120°00′E) to Pegunungan Latimojong (03°30′S, 121°23′E) in the south—the west-central region (or western mountain block) of Sulawesi's central core—and an altitudinal range from 350 m in tropical lowland evergreen rain forest to 2800 m in upper montane forest habitats (see gazetteer for *P. topapuensis* and map in fig. 11). Although collection sites are spotty throughout this extensive region, *P. topapuensis* likely occurs everywhere in suitable forested habitats. Whether it inhabits forests along the western coastal lowlands (between about 1° and 3°30′S) is unknown, for no specimens of squirrels have been collected there. This region has never enjoyed surveys documenting the diversity of small mammal species. If *P. topapuensis* does descend to altitudes along the coastal plain just above sea level, it would be in forests covering these western lowlands bordering the Makassar Strait. On the other hand, possibly a different member of the *P. leucomus* groups inhabits those coastal forests. A good candidate is *P. weberi*, which is currently known from only two places east of the mountains in the lowlands fringing Teluk Bone. Conceivably, the species could be found in the lowlands flanking the southern margins of the central mountains and all along the western coast in lowland forests fringing the western flanks of the mountainous central region.

We cannot, however, dismiss a speculation that *P. topapuensis* may inhabit only foothills and mountains but not along the coast. Along Musser's transect in the northern portion of Sulawesi's southern core, he collected different species of squirrels from 290 m to the summit of Gunung Nokilalaki above 2200 m. The lowest elevation was along Sungai Oha Kecil, a tributary of the Sungai Miu and downriver from the camp at 350 m, which is the lowest record for *P. topapuensis*. Musser trapped along the Oha Kecil and in the adjacent hillsides employing long traplines that included many Conibear traps. He caught only the large-bodied *Rubrisciurus rubriventer* and the much smaller-bodied *Prosciurillus murinus* (see those respective gazetteers). No examples of *P. topapuensis* were encountered or even seen in the forest until the Sungai Miu camp and higher along the Sungai Sadaunta. We need more inventories of tree squirrels derived from transects extending into coastal lowlands elsewhere along the western coastal flanks of the west-central mountain block.

No specimens of squirrels in the *P. leucomus* group are available from the highlands between the Danau Lindu region and approximately 80 km to the north in the basal portion of the northern peninsula at Bumbarujabu (00°43′S, 120°04′E). The sample from Bumbarujabu is *P. leucomus*, exhibiting a very different pelage pattern and found only on the northern peninsula (see section on comparisons). We do not know where the geographic range of *P. topapuensis* ends in this unsurveyed interval and that of *P. leucomus* begins.

The forested lowlands east of the mountainous range of *P. topapuensis*, from south of Parigi along the fringing eastern coast to the eastern portion of the central core, are inhabited by populations of *P. alstoni*, another member of the *P. leucomus* group characterized by a color pattern strikingly different than seen in *P. topapuensis* (see comparisons). In the Mapane region at the southern margin of Teluk Tomini, the distance between collection sites for *P. alstoni* at Mapane and Pinedapa and to the west in the mountains at Rano Rano where *P. topapuensis* was encountered is only about 20 airline km. Other collection sites for each species are much farther apart—where the western range boundary for *P. alstoni* lies relative to the eastern boundary for *P. topapuensis* is not known (see the account of *P. alstoni* for details). The eastern flanks of the mountainous central core—generally west of a line extending from the Mapane region in the north through the west side of Danau Poso to the western foothills in the south in the areas west of Masamba, Palopo, and the eastern flanks of Pegunungan Latimojong may delimit the eastern range boundary for *P. topapuensis*, at least where suitable forest habitats persist and in the past when forest cover was less altered than at present.

In the Masamba and Palopo lowlands west of the central mountains, the indigenous member of the *P. leucomus* group is *P. weberi*, not *P. alstoni* (see that account). In this area the mountainous range of *P. topapuensis* sits adjacent to that of lowland *P. weberi*, which has been collected only around Masamba (02°34′S, 120°19′E) and Palopo (03°01′S, 120°13′E).

The southern flanks of Pegunungan Latimojong and the adjacent highlands to the west likely mark the southern boundary of the range of *P. topapuensis*. This end of the west-central mountainous core of Sulawesi is separated from the southern portion of the southwestern peninsula by the Tempe Depression, a lowland trough containing flood lakes over which a river may have flowed in the past. One of the lakes, Danau Tempe, "... appears to be a remnant of an ancient strait that formerly separated the southern arm of the Toraja highlands [Pegunungan Latimojong and highlands to the north] from southern Sulawesi" (Whitten et al., 1987: 259). No modern specimens of the *P. leucomus* group have been collected south of the Tempe Depression, but a member once occurred there and that population is represented by a subfossil fragment (see account of *Prosciurillus* sp.).

Available voucher specimens of *Prosciurillus topapuensis* identify it as part of the mammalian fauna endemic to the west-central region in Sulawesi's central core. This is the area of foothills, interior valleys, and mountain peaks lying west of Danau Poso, and extending from the Palu area in the north to Pegunungan Latimojong in the south. In addition to *P. topapuensis*, samples of three species of shrews (*Crocidura*), one or two primates (*Tarsius*), a ground squirrel (*Hyosciurus*), and 13 species of murid rodents have been collected so far only from the west-central foothills, valleys, and mountains (table 25).

DESCRIPTION: *Prosciurillus topapuensis* has dark brown upperparts, black ear tufts, and dark gray underparts washed with buff or silver. The squirrel is similar to *P. leucomus* and *P. alstoni* in body size and most physical proportions (length of head and body, 151–190 mm; length of hind foot, 40–49 mm; length of ear, 15–21 mm; weight, 130–210 g; see tables 15, 16). Thickness and color of the fur covering upperparts of head and body are also similar; all three species possess a uniformly thick coat (12–15 mm) that is dark brown flecked with black and orange along midline of the body from forehead to base of tail, but grading into a slightly paler brown spotted with black and pale buff along sides of the head, body, forelegs, and hind legs. Dorsal surfaces of the front and hind feet may be the same color as the head and back, slightly darker, or slighter paler (buffy gray). Coloration of the body fur results from the mixture of dark gray curly underfur; longer overfur composed of hairs each of which is blackish gray with a subterminal orange or buffy band and black tip; and black guard hairs barely projecting beyond the overhair layer (about 5 mm). Animals from high altitudes in montane forests tend to be slightly paler; the subterminal bands on the overhairs are buff instead

TABLE 25
Mammal Species Currently Recorded Only from the West-Central Region in Sulawesi's Central Core[a]

Taxon	Lowland evergreen rain forest	Lower and/or upper montane forest
Shrews		*Crocidura*, n. sp. A (related to *C. elongata*)
		Crocidura, n. sp. B
		Crocidura musseri
Primates	*Tarsius lariang*	*Tarsius pumilus*
	Tarsius dentatus/*Tarsius dianae*	
Squirrels	*Prosciurillus topapuensis*	*Prosciurillus topapuensis*
		Hyosciurus heinrichi
Rats		*Sommeromys macrorhinos*
	Crunomys celebensis	
		Eropeplus canus
		Tateomys rhinogradoides
		Tateomys macrocercus
		Melasmothrix naso
		Taeromys hamatus
	Maxomys, n. sp. A	*Maxomys*, n. sp. A
	Maxomys, n. sp. B	
		Haeromys, n. sp.
	Bunomys, n. sp.	
		Margaretamys parvus
		Margaretamys elegans

[a]The west-central region (or western mountain block) consists of the highlands forming the western portion of Sulawesi's central core. It is that region of foothills, peaks, and interior valleys roughly west of Danau Poso, and extending from the Palu area in the north to Pegunungan Latimojong in the south.

Data are derived from published (Musser, 1981, 1987; Musser and Carleton, 2005; Musser and Dagosto, 1987; Musser and Durden, 2002; Musser and Holden, 1991; Ruedi, 1995; Merker and Groves, 2006) and unpublished results of research by Musser.

Additional information covering certain species is provided in the footnotes to table 31.

of orange, and the dorsal coat slightly thicker.

The dorsal background forming upperparts of *P. topapuensis* is interrupted by a buffy ring encircling each eye, a buffy muzzle and chin, and black ear tufts. Glossy black hairs cover the medial surface of each pinna and extend beyond its margin to form a short (4–8 mm) black tuft, closely similar in configuration to the tufts in the samples of *P. leucomus* from the northern peninsula. Within the sample, the tufts vary in their expression, and are so reduced in one specimen (a few black hairs) as to be inconspicuous—this squirrel has a uniform dark brown back with buff and black highlights. *Prosciurillus topapuensis* lacks any sign of nape patches behind the ears—fur covering top and sides of the neck is indistinguishable in color from the rest of the upperparts—or a black middorsal stripe.

Fur covering the underparts from chin to base of the tail is moderately thick (up to 10 mm) and very dark gray with silver highlights (dark grayish white) or washed with pale buffy or ochraceous hues. The overhairs are dark gray for two-thirds of their lengths and unpigmented at the tips or retain pale buffy or ochraceous bands. Dark grayish white venters are infrequent in our sample of *P. topapuensis*, and even those specimens with primarily silver-tinted venters exhibit small buffy infusions on the chest. The ventral coloration hardly contrasts with that of the upperparts.

The tail of *P. topapuensis* is shorter than the length of the head and body (LT/LHB = 84%–96%, see table 16) and is covered in long hairs, each patterned by alternating black and buffy or orange bands. The overall effect is rings of black and buff with buffy and short black bands outlining margins of

the tail and long black hairs forming a black terminal tuft. The ventral surface of the tail resembles the upperparts, dark brown with orange and black highlights bordered by black and buffy margins. Overall coloration of the tail is similar to that seen in *P. leucomus*, *P. alstoni*, and *P. weberi*, but somewhat browner.

As with the other members of the *P. leucomus* group, female *P. topapuensis* have three pairs of teats, one abdominal pair and two inguinal pairs. One female with enlarged teats exhibited a placental scar in the right uterine horn; other females examined, although adult, showed no reproductive activity.

Views of the skull are provided in figures 12–14; cranial and dental measurements are summarized in tables 17 and 26.

COMPARISONS: *Prosciurillus topapuensis* requires comparisons with *P. leucomus*, which ranges to the north throughout the northern peninsula, and *P. alstoni* and *P. weberi*, both occurring in lowlands adjacent to the mountainous distribution of *P. topapuensis*. See the account of *P. alstoni* for contrasts between it and *P. topapuensis*; here we describe differences between *P. topapuensis* and the other two species.

Prosciurillus topapuensis* and *P. leucomus: Body size is comparable in the two species, but the tail averages shorter relative to length of head and body in *P. topapuensis* (tables 15, 16). Representatives of *P. topapuensis* from lower altitudes show a dorsal coat similar in thickness and coloration to that of *P. leucomus*, but individuals from upper montane forests have a thicker, slightly duller coat, the orange and bright buffy bands of the hairs giving the lowland squirrels their speckling against the brown background are slightly paler in the montane animals. Both species have black ear tufts, but those of *P. topapuensis* vary in size among the samples, ranging from being prominent (like those in samples of *P. leucomus*) to showing only traces of black on the ears of a very few individuals; every specimen of *P. leucomus* has prominent black tufts. The inner surface of each ear at the base of the tuft is the same color as the rest of the head and not bright ochraceous as seen in *P. leucomus*. Fur behind the ears on the neck of *P. topapuensis* is the same color as the head and back, which is strikingly unlike that region in most specimens of *P. leucomus* where the neck is marked by conspicuous whitish nape patches. Finally, all examples we studied of *P. topapuensis* show a dark gray coat highlighted with silver or hues of buff and ochraceous covering the underparts; the ventral fur of *P. leucomus* ranges from reddish orange to ochraceous (table 12). Specimens of *P. topapuensis* appear monochromatic (brownish gray everywhere), those of *P. leucomus* are bicolor (dark brown upperparts, reddish underparts).

As with all members of the *P. leucomus* group, skulls of *P. topapuensis* and *P. leucomus* closely resemble one another in general size and shape but contrast in average size and proportions of some dimensions. Except for length of nasals, breadth of rostrum, and height of braincase, cranial and dental dimensions average less in the sample of *P. topapuensis* compared with *P. leucomus* (table 17). That difference can also be visualized by results of multivariate analyses illustrated in an ordination showing specimen scores projected onto the first and second principal components extracted from principal-components analysis (fig. 24). The group of scores representing geographic samples of *P. leucomus* overlaps with the cloud of points identifying specimens of *P. topapuensis* along the first component (an estimate of size) but is pushed slightly farther to the right by the moderate to high positive loadings of all variables except height of braincase (table 27). Fewer variables strongly influence the distribution of scores along the second axis, which reflects shape distinctions. Compared with *P. topapuensis*, the northern peninsular species *P. leucomus* has a relatively wider interorbit, mastoid region, and bony palate, and longer orbit and auditory bulla, but relatively shorter nasals, diastema, and tooth row, and narrower rostrum. These are subtle shape differences but some of them, especially the narrower interorbit and shorter orbit of *P. topapuensis*, are visually apparent when skulls of each species are compared side-by-side.

Prosciurillus topapuensis* and *P. weberi: These two species are similar in body size and contrast in relative tail length along with

TABLE 26
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of *Prosciurillus topapuensis*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Sungai Miu-Sungai Sadaunta $N = 9$	Gunung Kanino $N = 5$	Gunung Lehio $N = 9$	Besoa region $N = 5$	Rano Rano $N = 11$	Pegunungan Latimojong $N = 11$
ONL	46.6 ± 0.53 (45.5–47.2)	45.0 ± 0.77 (43.8–45.8)	44.3 ± 0.85 (43.1–46.1)	44.3 ± 1.21 (42.8–45.9)	43.7 ± 0.85 (42.0–45.0)	43.5 ± 0.66 (42.5–44.5)
CBL	42.0 ± 0.78 (40.3–43.0)	40.6 ± 0.94 (39.2–41.5)	40.1 ± 0.79 (38.4–40.9)	39.6 ± 1.08 (38.9–41.4)	39.2 ± 1.13 (37.3–40.5)	38.6 ± 0.64 (37.2–39.7)
ZB	27.1 ± 0.57 (26.3–28.0)	27.3 ± 0.58 (26.5–27.3)	26.4 ± 0.70 (25.5–27.4)	26.1 ± 0.66 (25.5–27.2)	25.8 ± .65 (24.4–26.5)	26.3 ± 0.58 (25.5–27.3)
IB	16.7 ± 0.27 (16.2–17.0)	16.1 ± 0.51 (15.5–16.9)	16.0 ± 0.51 (15.0–16.7)	15.6 ± 0.58 (14.8–16.4)	15.8 ± 0.68 (14.8–17.2)	15.4 ± 0.46 (14.4–16.2)
LN	13.0 ± 0.48 (12.0–13.5)	13.2 ± 0.73 (12.3–14.3)	12.7 ± 0.50 (12.1–13.5)	12.2 ± 0.48 (11.5–12.6)	12.6 ± 0.73 (11.5–13.8)	12.5 ± 0.44 (11.7–13.4)
LR	20.7 ± 0.37 (20.2–21.3)	19.8 ± 0.77 (18.9–20.5)	19.4 ± 0.62 (18.3–20.1)	19.2 ± 0.71 (18.2–20.0)	19.2 ± 0.75 (18.0–20.2)	19.0 ± 0.45 (18.5–20.0)
BR	8.9 ± 0.60 (8.0–9.7)	8.3 ± 0.48 (7.6–8.9)	8.9 ± 0.49 (8.2–9.4)	8.2 ± 0.51 (7.7–8.8)	8.3 ± 0.48 (7.3–9.0)	8.7 ± 0.42 (8.2–9.4)
MB	19.3 ± 0.52 (18.5–20.0)	18.8 ± 0.72 (18.0–19.9)	18.6 ± 0.46 (18.0–19.5)	18.1 ± 0.31 (17.7–18.5)	18.1 ± 0.40 (17.2–18.5)	18.1 ± 0.22 (17.7–18.4)
HBC	15.3 ± 0.46 (14.9–16.1)	15.6 ± 0.45 (15.0–16.1)	15.1 ± 0.34 (14.6–15.5)	15.2 ± 0.13 (15.0–15.3)	15.2 ± 0.43 (14.6–16.0)	15.2 ± 0.56 (14.3–15.9)
LO	9.9 ± 0.30 (9.4–10.3)	10.0 ± 0.31 (9.6–10.3)	9.7 ± 0.45 (8.8–10.1)	9.4 ± 0.47 (9.1–10.2)	9.2 ± 0.23 (8.9–9.5)	9.6 ± 0.24 (9.2–10.2)
LD	9.5 ± 0.45 (8.8–10.1)	9.3 ± 0.43 (8.8–9.7)	8.4 ± 0.24 (8.0–8.9)	9.0 ± 0.29 (8.5–9.2)	8.9 ± 0.55 (8.0–9.5)	8.7 ± 0.37 (8.1–9.2)
LBP	12.6 ± 0.66 (12.0–13.6)	12.1 ± 0.32 (11.6–12.7)	12.3 ± 0.47 (11.7–13.0)	11.7 ± 0.44 (11.3–12.4)	12.1 ± 0.59 (11.1–12.9)	12.0 ± 0.41 (11.4–12.7)
PPL	17.9 ± 0.56 (17.0–18.8)	16.9 ± 0.78 (16.0–17.7)	17.0 ± 0.39 (16.3–17.7)	17.2 ± 0.55 (16.7–18.1)	16.4 ± 0.56 (15.6–17.3)	16.4 ± 0.49 (15.8–17.3)
BBP	9.7 ± 0.38 (9.0–10.2)	9.6 ± 0.20 (9.3–9.8)	9.9 ± 0.24 (9.6–10.2)	9.9 ± 0.34 (9.5–10.4)	9.4 ± 0.25 (9.0–9.9)	9.3 ± 0.25 (15.8–17.3)
LB	8.0 ± 0.24 (7.7–8.5)	7.7 ± 0.22 (7.4–8.0)	7.4 ± 0.30 (7.0–7.8)	7.4 ± 0.48 (7.0–7.9)	7.6 ± 0.30 (7.1–8.0)	7.4 ± 0.20 (7.0–7.7)
CLPMM	7.5 ± 0.25 (7.1–7.9)	7.1 ± 0.19 (6.8–7.3)	7.7 ± 0.26 (7.2–8.0)	7.5 ± 0.29 (7.0–7.7)	7.2 ± 0.20 (6.8–7.5)	7.3 ± 0.22 (7.0–7.7)

fur texture in much the same way as seen between *P. topapuensis* and *P. leucomus*. The former has a shorter tail relative to length of head and body, duller upperparts, and dark grayish buff or grayish white underparts instead of the reddish orange covering typical of *P. weberi*. Both species lack nape patches, both exhibit black ear tufts, but the back of *P. topapuensis* is unmarked by a black middorsal stripe, which is so conspicuous on all examples of *P. weberi*.

The ordination of specimen scores projected onto the first and second principal components extracted from principal-components analysis in figure 25 summarizes our multivariate analysis of the cranial and dental variables we employed. No separation of the scores representing specimens of each species is apparent along the first axis, a general estimate of size, partly because the sample of *P. weberi* is so small compared with that of *P. topapuensis*, and partly because of the breadth of individual and geographic variation in that species as indicated by the wide scatter of points along the first component, which is influenced by the moderate to high positive loadings of most variables (table 28). The few variables primarily contributing to

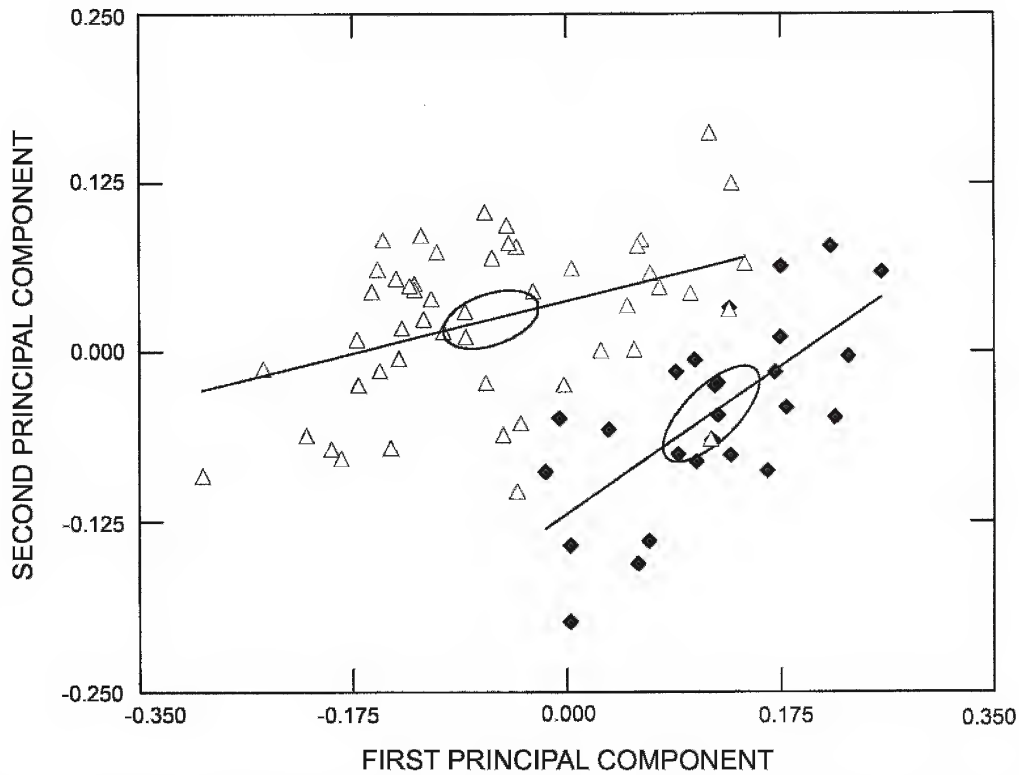

Fig. 24. Specimen scores representing population samples of *Prosciurillus topapuensis* from the central core of the island (empty triangle, $N = 50$) and *P. leucomus* from the northern peninsula (filled diamond, $N = 26$) projected onto the first and second principal-components extracted from principal-components analysis. The ellipses outline 95% confidence limits for the specimen scores forming each cluster. Equations for the regression lines are: *P. leucomus*, $Y = 0.621X-0.120$ ($F = 22.07$, $P = <0.01$); *P. topapuensis*, $Y = 0.222X+0.038$ ($F = 9.25$, $P = <0.01$). The Y-intercepts of each regression line of the second principal component on the first component are significantly different (-0.120 versus $+0.038$; $F = 28.31$, $P = <0.001$). See table 27 for correlations and percent variance.

the spread of scores that form two nearly separate constellations along the second axis reflect contrasts in shape. *Prosciurillus weberi* has a relatively broader rostrum compared with *P. topapuensis* and relatively shorter nasals and tooth rows. This analysis needs to be revisited employing a much larger sample of *P. weberi* than is currently available.

GEOGRAPHIC VARIATION: Every example of *P. topapuensis* from the west-central mountain block is immediately recognizable by its short and black ear tufts, unpatterned neck and back, and very dark grayish white or grayish buff underparts. Variation in color patterning over the fur covering head and body appears to be altitudinal and individual rather than regional. Examples from high altitudes, usually in upper montane forests, have slightly thicker and duller upperparts than those taken in the foothills and lower places. Extent of the ear tufts range from being conspicuous on most squirrels to nearly hidden in the fur surrounding the ears in a very few specimens, and underparts range from dark gray speckled or washed with buff or ochraceous to dark gray lightly sprinkled with white (appearing as silvery highlights); these expressions in ear tufts and tone of underparts occur within the same sample as well as among population samples and do not appear to be correlated with altitude.

Body size may vary with altitude. Along Musser's transect, the only line along which samples have been collected that extends

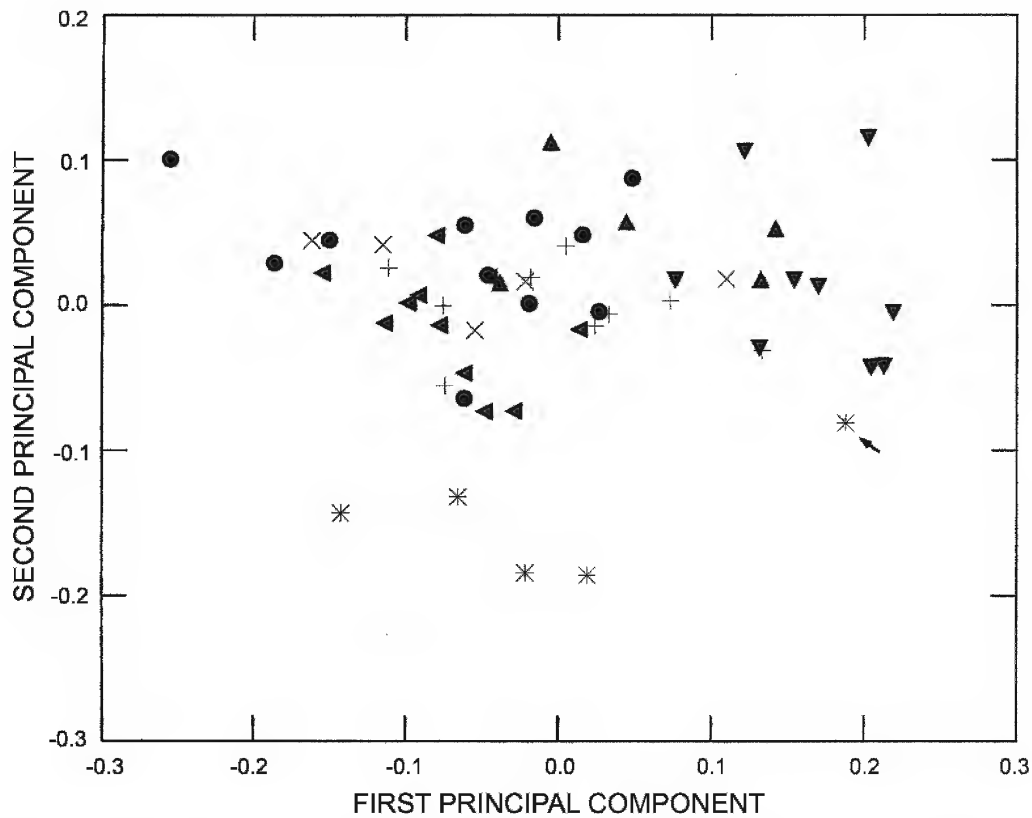

Fig. 25. Specimen scores representing population samples of *Prosciurillus topapuensis* and *P. weberi* (star, $N = 5$) projected onto the first and second principal components extracted from principal-components analysis. Symbols identifying samples of *P. topapuensis* are: filled circle = Rano Rano ($N = 11$); x = Besoa-Lindu trail ($N = 5$); cross = Gunung Lehio ($N = 9$); filled upright triangle = Gunung Kanino ($N = 5$); filled inverted triangle = Sungai Miu and Sungai Sadaunta ($N = 9$); filled left-pointing triangle = Pegunungan Latimojong ($N = 11$). Arrow identifies score for the lectotype of *weberi*. See table 28 for correlations and percent variance.

from tropical evergreen rain forests in the lowlands to montane rain-forest habitats in adjacent highlands, squirrels from Sungai Miu and Sungai Sadaunta, in lowland evergreen rain forest between 350 and 915 m, average slightly greater in many body and cranial dimensions than do those collected from higher altitudes along the transect, and from mountains east and south of the region where Musser worked (tables 16, 26).

Results of multivariate analyses of cranial and dental variables as presented in the ordination of specimen scores projected onto the first and second principal components extracted from principal-components analysis in figure 26A reflect the altitudinal variation in size and also identifies a regional component. Covariation in nearly all variables contributes to the spread of scores along the first axis (table 29), reflecting increasing size from left to right, with points for most geographic montane samples intermingled, and scores representing samples from Sungai Miu and Sungai Sadaunta (350–915 m) anchoring the right sector of the constellation. Scores representing squirrels collected between 1400 and 1500 m on nearby Gunung Kanino are sprinkled through the cloud from the right to the center.

Scores for specimens from Gunung Lehio (crosses in fig. 26A), just south and east of Musser's transect, are scattered in the con-

TABLE 27
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus topapuensis* with Those of *Prosciurillus leucomus*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 24.

Variable	PC1	PC2
ONL	0.027	0.003
CBL	0.032	0.004
ZB	0.032	−0.006
IB	0.054	−0.018
LN	0.021	0.025
LR	0.041	0.009
BR	0.028	0.043
MB	0.029	−0.011
HBC	0.002	−0.002
LO	0.044	−0.022
LD	0.033	0.026
LBP	0.029	0.010
PPL	0.035	0.002
BBP	0.024	−0.014
LB	0.036	−0.013
CLPMM	0.020	0.017
Eigenvalues	0.017	0.005
Percent variance	47.745	14.314

TABLE 28
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus topapuensis* with the Sample of *Prosciurillus weberi*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 25.

Variable	PC1	PC2
ONL	0.028	0.003
CBL	0.033	0.008
ZB	0.023	0.007
IB	0.030	0.009
LN	0.030	0.022
LR	0.037	0.009
BR	0.034	−0.052
MB	0.021	−0.002
HBC	0.008	0.013
LO	0.026	−0.005
LD	0.042	−0.03
LBP	0.029	0.010
PPL	0.032	−0.011
BBP	0.014	0.000
LB	0.028	0.001
CLPMM	0.010	0.016
Eigenvalues	0.013	0.004
Percent variance	39.660	13.028

stellation from left to right along the first component and also tend to lay along the outskirts of the larger cluster from the perspective of the second axis. This alignment suggests the sample from Gunung Lehio to have a relatively wider rostrum and bony palate, longer tooth row, and shorter diastema as compared to specimens in the other geographic samples (table 29).

We can easily describe the results diagrammed in the principal-components ordination but assessing the significance of the pattern is difficult without additional samples. Certainly variation in size of skull concomitant with age reflects one component of the broad spread of scores along the first axis—samples are mixed, containing the range from young adults to old adults. Comparing larger samples, each composed of the same relative age, may better resolve the true pattern of altitudinal and regional variation. Musser's small samples from low altitudes are highlighted in the cluster of scores, suggesting that populations in lowlands and foothills may average larger in body size than those living at higher altitudes in montane forest habitats. This aspect of variation gleaned from study of material at hand needs to be tested by larger samples collected along transects from different regions in the mountainous western section of Sulawesi's central core. Finally, some populations of *P. topapuensis* may be partially isolated from one another by large rivers or other kinds of geographic barriers, which might be revealed by a greater density of sampling over the geographic range that we have described.

We were tantalized by the average differences in body size between the two samples of squirrels, one from 350–915 m and the other from higher altitudes, because among other groups of mammals, especially murid rodents, there is a pattern of closely related species replacing each other with altitude generally concordant with forest type in the western mountain block of Sulawesi's central core (table 31). One set of shrews (*Crocidura*), bats (*Thoopterus*), tarsiers (*Tarsius*), and squirrels (*Hyosciurus*), and three sets of murid rodents (*Bunomys*, *Haeromys*, and *Margaretamys*) collected along Musser's

transect, from the lowlands in the Sungai Miu region to the summit of Gunung Nokilalaki in montane forests provide examples. The lowland species in each of these sets is very distinctive compared with their respective montane relatives; the dissimilarity is expressed in body size, fur coloration, and marked contrasts in cranial conformations along with cranial and dental dimensions.

No such marked morphological differences contrast squirrels in the samples of *P. topapuensis* from Sungai Miu and Sungai Sadaunta compared with those collected on the slopes of Gunung Kanino or even higher in other parts of the western mountain block. Specimens in each set of samples are indistinguishable in fur coloration and expression of black ear tufts, those from the lower altitudes simply average slightly larger in body size and have slightly brighter upperparts. Apparently the same species ranges from foothills to higher in the mountains, which parallels the altitudinal distributions of two species of *Crocidura*, one macaque, two other tree squirrels, and six species of murid rodents (table 31).

ECOLOGY: *Prosciurillus topapuensis* inhabits the upper canopy of primary forest. In all the different altitudinal forest formations, the squirrels mostly remain in crowns and woody vines forming the upper canopy. They are active in the mornings and afternoons during sunny days, but might be active all day long on cloudy days. They travel through the upper canopy, but come to the ground occasionally, especially in places where the canopy is broken. When on the ground, the squirrels run on trunks and limbs lying on the forest floor and regularly cross streams and rivers along bridges formed by branches of live trees arching over the water as well as rotting tree trunks and limbs and palm trunks connecting opposite stream terraces. Most of Musser's specimens were trapped on these kinds of river and stream crossings (habitats at trap sites are summarized in table 32).

Musser encountered *P. topapuensis* all along the transect line, from Sungai Miu at 350 m to the summit of Gunung Nokilalaki at 2300 m (see photograph of forest on Gunung Kanino in fig. 27), from lowland evergreen rain forest to upper montane rain forest, and through a range of ambient temperatures (table 2) and habitats—forested stream terraces, hillsides, and ridgetops. Although wary and quiet in the forests around Tomado at 1000 m, and usually seen only in tree crowns forming the high canopy, the squirrels were aggressive and loud elsewhere along the transect line. At higher altitudes along the Sungai Tokararu and slopes of Gunung Kanino (1150–1500 m), for example, *P. topapuensis* was common, aggressively vocal, and unwary—Musser saw squirrels there every day. On several different days he would be walking along the trapline and every time he stopped to rebait a trap a squirrel would begin its loud, resonant, scolding chatter, always positioned just out of reach above his head. The squirrel remained quiet as long as Musser kept walking, but once he stopped the scolding began again until he left the area. On one occasion, a squirrel was in the crown of an understory tree isolated from nearby trees. To get out of the tree, the squirrel had to come to the ground but would not do so while Musser was there. It would scamper out to the end of a branch, stop and stare at Musser, then run to a different branch, all the time its tail twitching spastically with each raspy chuck. On another day, a squirrel left the upper canopy descending to the trunk where it stopped, splayed against the bark, head down, and tail flipping in agitated undulations with each loud chatter. It scolded for one or two minutes, then would run back up into the crown and disappear from sight. In addition to human presence, the squirrels were very sensitive to human voices, the sounds of trees falling in the forest, or even a limb hitting the ground, and the sights of hawks and eagles—all elicited a cacophony of strident loud chatter.

The sound of rain approaching in the forest also prompted alarm calls from squirrels and some birds. After the clouds build up and the sky darkens, and just before the torrent begins there is a period of absolute silence in the forest, shattered only by birdsong and a squirrel's resonant chucks. The squirrels call individually, not in chorus, and cease as the first drops splatter against the leaves, signaling the more intense approaching rain, which passes through the

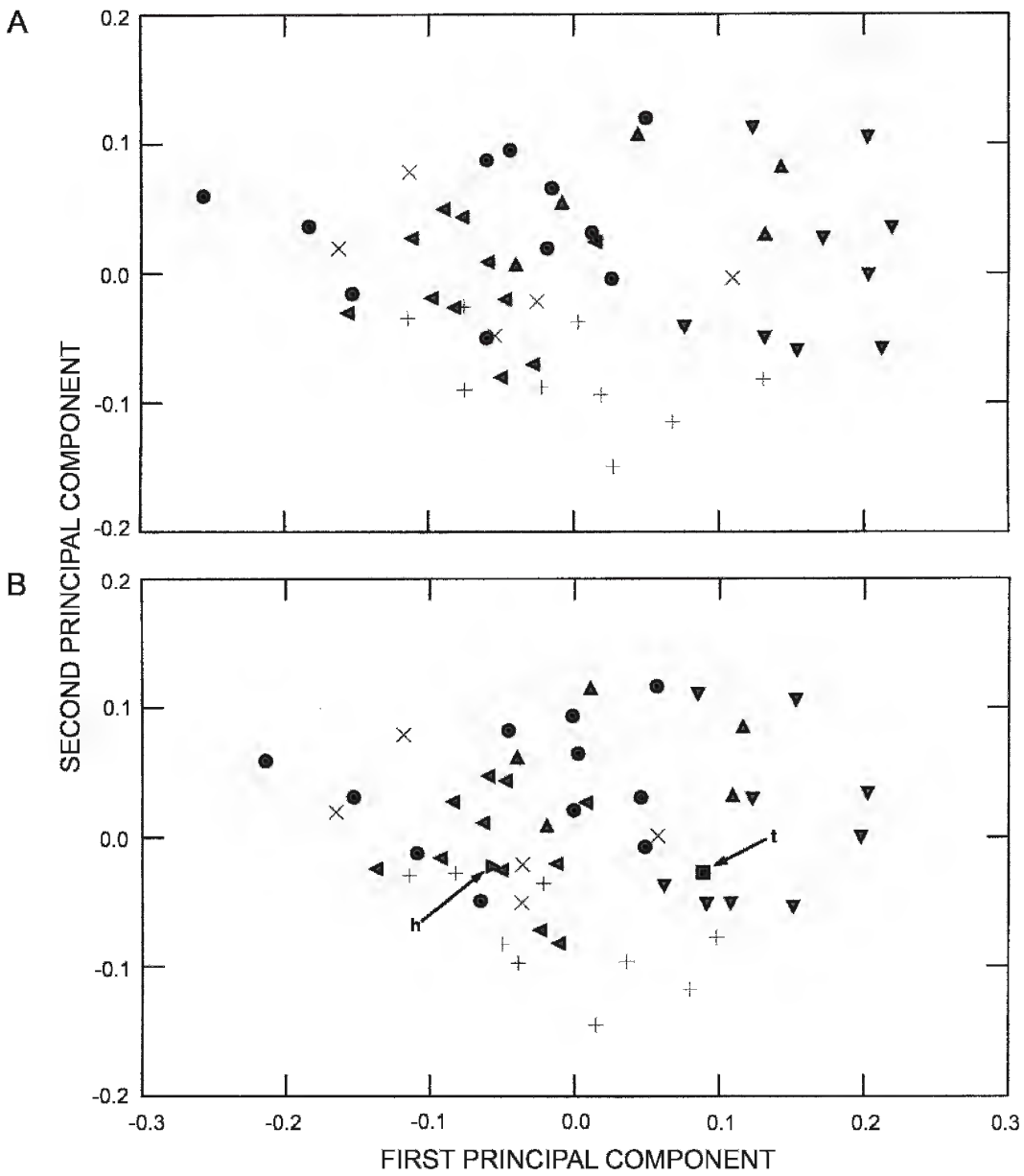

Fig. 26. Specimen scores representing six population samples of *Prosciurillus topapuensis* projected onto the first and second principal components extracted from principal-components analysis. Symbols identifying samples are: filled circle = Rano Rano (N = 11); x = Besoa-Lindu trail (N = 5); cross = Gunung Lehio (N = 9); filled upright triangle = Gunung Kanino (N = 5); filled inverted triangle = Sungai Miu and Sungai Sadaunta (N = 9); filled left-pointing triangle = Pegunungan Latimojong (N = 11). **A**: All cranial and dental variables are represented, but holotypes of *topapuensis* and *hirsutus* are excluded. See table 29 for correlations and percent variance. **B**: Includes the holotypes of *topapuensis* ("t" and filled square) and *hirsutus* ("h" and filled right-pointing triangle) but because these specimens are damaged only 11 cranial and dental variables could be employed. See table 30 for correlations and percent variance.

TABLE 29
Results of Principal-Components Analysis of Population Samples of *Prosciurillus topapuensis*
All variables are employed, but the holotypes of *topapuensis* and *hirsutus* are excluded because the skulls are damaged. Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 26A.

Variable	PC1	PC2
ONL	0.028	0.001
CBL	0.034	0.003
ZB	0.021	−0.004
IB	0.028	−0.000
LN	0.029	0.010
LR	0.037	0.002
BR	0.034	−0.041
MB	0.022	−0.004
HBC	0.006	0.003
LO	0.025	−0.003
LD	0.044	0.033
LBP	0.028	0.004
PPL	0.035	−0.001
BBP	0.010	−0.020
LB	0.030	0.001
CLPMM	0.009	−0.028
Eigenvalues	0.013	0.004
Percent variance	43.240	14.035

TABLE 30
Results of Principal-Components Analysis of Population Samples of *Prosciurillus topapuensis*
Fewer variables are used than listed in table 29 to accommodate the damaged holotypes of *topapuensis* and *hirsutus*. Principal components are extracted from a covariance matrix of log-transformed values for 10 cranial and 1 dental variable; see figure 26B.

Variable	PC1	PC2
IB	0.026	0.001
LN	0.031	0.009
LR	0.037	0.002
BR	0.038	−0.041
MB	0.019	−0.003
HBC	0.005	0.003
LD	0.043	0.033
LBP	0.031	0.003
BBP	0.007	−0.019
LB	0.030	0.001
CLPMM	0.007	−0.027
Eigenvalues	0.009	0.004
Percent variance	38.814	17.743

forest like a moving wet curtain. Several times Musser saw a squirrel on a large woody vine in the upper canopy calling in a long series of chattering chucks, then dart into a hole in the nearest tree just before the first drops were felt.

Musser looked for leaf nests but never found them. At one camp he passed a tall strangler fig on the way to check traps. The host tree had long since decayed and the enclosing trunk was filled with debris and leaf litter, held tightly by the criss-cross patterns of ropy trunk. Each day he would see a pair of squirrels in the crown, running over the upper trunk, limbs, and along the huge woody vines encircling the trunk. Periodically they would disappear into a space between the latticework, and then reemerge. One evening he watched them chase each other, feed on figs, and eventually disappear out of sight inside the trunk. Tall strangler figs are common in lowland rain forest and offer numerous sites for nests within the debris-filled hollows. Likely, cavities in other kinds of trees are also used for nest sites by *P. topapuensis*.

Judged by contents of stomachs, the diet of *P. topapuensis* consists of soft fruits, especially figs, some seeds, and arboreal insects (table 32). All the different fruits were thoroughly masticated, and only figs could be positively identified (pieces of rind and endosperm with tiny seeds attached). The insects consisted of small adult beetles (represented by fragments of wings, elytra, legs, and sclerites), macrolepidopteran caterpillars (whole or chewed into pieces) gleaned from surfaces of leaves and bark, and cockroaches (indicated by legs, antennal segments, wings, and masticated bodies). Beetles were uncommon in stomachs, but the caterpillars must be a favorite prey. Remains were found in many stomachs, and of these one (AMNH 225501) was distended with large (20–30 mm long) macrolepidopteran caterpillars, many of them still in one piece. The stomach of another squirrel (AMNH 225504) was packed with smaller (10–15 mm long) macrolepidopteran larvae, whole and in pieces. Both squirrels were caught on Gunung Kanino above 1400 m (table 32). Cockroaches are in the trees and on the ground. Soft fruits and insects also

TABLE 31
Tropical Lowland Evergreen Rainforest Species, Their Montane Forest Replacements, and the Species Found in Both Lowland and Montane Forests in the West-Central Region of Sulawesi's Central Core[a]

Taxon	Lowland evergreen rain forest	Lower and upper montane rain forests	Lowland evergreen and montane rain forests
Shrews	*Crocidura elongata*	*Crocidura*, n. sp. A	
			Crocidura nigripes
			Crocidura rhoditis
Bats	*Thoopterus nigrescens*[b]	*Thoopterus*, n. sp.	
Primates	*Tarsius lariang*, *Tarsius dentatus/dianae*[c]	*Tarsius pumilus*	
			Macaca tonkeana
Squirrels	*Hyosciurus ileile*[b]	*Hyosciurus heinrichi*	
			Rubrisciurus rubriventer (up to lower montane forest only)
			Prosciurillus topapuensis
			Prosciurillus murinus
Rats	*Bunomys*, n. sp.	*Bunomys penitus*	*Bunomys chrysocomus*
	Bunomys andrewsi		
	Haeromys minahassae	*Haeromys* sp.	
	Margaretamys beccarii	*Margaretamys parvus*	
		Margaretamys elegans	
	Maxomys hellwaldii, *Maxomys* sp. B	*Maxomys dollmani*	*Maxomys* sp. A (up to lower montane forest only)
			Maxomys musschenbroekii
			Paruromys dominator
			Rattus marmosurus
			Rattus hoffmanni

[a]The west-central region (or western mountain block) consists of the highlands forming the western portion of Sulawesi's central core. It is that region of foothills, peaks, and interior valleys roughly west of Danau Poso, and extending from the Palu area in the north to Pegunungan Latimojong in the south.

Data are derived from published (Musser, 1981, 1987; Musser and Dagosto, 1987; Musser and Holden, 1991; Musser and Carleton, 2005; Merker and Groves, 2006) and unpublished results of research by Musser and colleagues, and Musser's observations in the field.

[b]Two pairs of species overlap in forest formations. *Thoopterus* sp. is sympatric with *T. nigrescens* near the upper limit of lowland evergreen rain forest near Sungai Tokararu at 1150 m (see map in fig. 4). The two species of *Hyosciurus* are parapatric in lower montane forest on Gunung Kanino.

[c]Four years ago, Groves (2005: 127) applied the name *dentatus* to the population of tarsiers occurring in the lowlands of central Sulawesi and regarded *Tarsius dianae* (Neimitz et al., 1991) as a synonym. Recently, Merker and Groves (2006) described *Tarsius lariang*, based on specimens obtained near Gimpu (01°38′S, 120°02′E, 400 m), just west of Lore-Lindu National Park in the west-central region of Sulawesi's central core, and postulate the range to extend from the Palu region in the north to the Toraja highlands or Tempe depression in the south, and from the coast along the Makassar Straight in the west to the western boundary of Lore-Lindu National Park in the east (voucher specimens come only from the vicinity of Gimpu). They consider landscapes to the east of the range to be occupied by *T. dianae* (which they acknowledge may be the same as the earlier described *T. dentatus*), those to the south on the southwestern peninsula to contain *T. tarsier*, with one or more unnamed species occurring elsewhere on the island.

comprise the diet of the genetic and geographic relative *P. alstoni*, but the range of insect groups encountered in stomachs of that species was greater than that recovered from stomachs of *P. topapuensis* (table 24).

ECTOPARASITES: *Prosciurillus topapuensis* is parasitized by a host-specific sucking louse, *Hoplopleura topapuensis*, n. sp. (described in a following section), as well as two species of flea (table 56). *Sigmactenus sulawesiensis*

Fig. 27. Habitat of *Prosciurillus topapuensis* in lower montane rain forest on Gunung Kanino, 1440 m. The large, darker tree in the center of the photograph is the oak *Lithocarpus glutinosus*. *Prosciurillus murinus* and *Rubrisciurus rubriventer* occupy this forest as does the ground squirrel *Hyosciurus ileile*. This elevation is close to the upper altitudinal limits of *R. rubriventer* and *H. ileile*. See table 2 for the range of ambient temperatures recorded during the sampling period. Photographed in 1975.

TABLE 32

Summary of Habitat at Trapping Sites, Stomach Contents, and Other Relevant Information for Specimens of *Prosciurillus topapuensis*

Collected by Musser in Central Sulawesi, 1973–1976 Collection locality, specimen number, elevation, and month and year of collection are included. Descriptions of the trapping sites and contents of stomachs, slightly edited, are from Musser's field journals (in mammalogy archives at AMNH). Three of the collection localities (Sungai Miu, Sungai Sadaunta, and Tomado) are in tropical lowland evergreen rain forest; lower montane rain forest describes the places on Gunung Kanino, and tropical upper montane rain forest the site on Gunung Nokilalaki. With one exception, all squirrels were caught during the day in Conibear traps (rats taken in the same traps were caught during the night). Unless noted differently, trapping sites were in primary forest formations.

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
Sungai Miu 224042 (1510)	350	Mar. 1974	On top of rotting trunk lying in forest understory next to small stream. **Stomach**: empty except for the few remains of a small adult beetle.
Sungai Sadaunta 224041 (1413)	675	Feb. 1974	5 ft above ground on dead tree limb projecting through understory of primary streamside forest. **Stomach**: partially filled with grayish red remains of large-seeded fig; pieces of small adult beetles (sclerites with tissue attached).
225581 (2059)	762	Sept. 1974	On wet, smooth and rotting trunk lying across stream near camp in streamside forest. A *Prosciurillus murinus* and a rat, *Maxomys musschenbroekii*, were taken in same spot. **Stomach**: full of reddish mash from a fig with large seeds; a small ant, and bits of sclerites from small adult beetle.
224582 (2037)	824	Sept. 1974	On wet, decomposing *Pigafetta* palm trunk lying across Sungai Sadaunta about 200 ft upstream from where *Rubrisciurus* ASE 2033 was trapped (see table 10). A *Prosciurillus murinus* was caught on same spot on a different day. **Stomach**: full of reddish mash of fig remains, with small seeds; no insects.
224583 (2194)	824	Oct. 1974	On rotten, wet wanga (*Pigafetta filaris*) palm trunk lying across Sungai Sadaunta in undisturbed streamside forest. *Prosciurillus murinus* and the rat, *Rattus hoffmanni* were taken at same spot. **Stomach:** nearly empty, remains of a soft fruit; no insects.
224584 (2119)	869	Oct. 1974	On half-shredded, rotting, and slick *Pigafetta* palm trunk lying across Sungai Sadaunta, extending from a low terrace (muddy, rocky, and eroded) on one side of stream across to the opposite rocky bank. A rat, *Bunomys* sp., was caught in same trap. A few feet upstream another rat, *Paruromys dominator*, was caught on a different trunk bridging the stream. *Prosciurillus murinus* was caught at same spot as ASE 2119 on a different day. **Stomach:** partially full of same reddish fig pulp and seeds found in other stomachs.
224585 (2223)	869	Oct. 1974	On large rotting trunk lying across stream connecting one forested terrace to the opposite stream terrace. Several examples of the rats *Paruromys dominator* and *Rattus hoffmanni* were trapped at same spot. **Stomach**: full of finely chewed fruit, some of it figs, along with remains of small macrolepidopteran caterpillars and a few small adult beetles.
224586 (2281)	915	Oct. 1974	On large, rotting trunk covered with moss, epiphytes, ferns, shrubs, and vines lying across stream, leaning from the bank on one side of stream to terrace on other side. **Stomach:** partially full of reddish brown mash from soft fruit.

TABLE 32
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
224587 (2325) 224588 (2345)	915	Nov. 1974	On limb of understory tree growing across ravine containing main upper tributary of the Sungai Sadaunta; base of the trunk is at edge of stream, with the trunk leaning over the water and its upper branches reclining on the opposite terrace. The main connecting limb (3–5 ft in diameter) on which the trap was placed is mossy, and the moss is trampled, indicating the limb to be used regularly; trap set about 7 ft from stream level. Examples of three kinds of squirrels (the ground squirrel, *Hyosciurus ileile*; the tree squirrels, *Rubrisciurus rubriventer* and *Prosciurillus murinus*) and an arboreal rat (*Rattus marmosurus*) were taken in the same spot. So three kinds of tree squirrels, one ground squirrel, and at least one species of arboreal murid used the same living pathway as a bridge over the stream.
226835 (4320)	915	Mar. 1976	Caught about 6:00 a.m. at same spot on limb of understory tree where *Prosciurillus topapuensis* ASE 2325 and ASE 2345 and other squirrels and rats were trapped in 1974. **Stomach**: distended with remains of tiny-seeded figs with remains of a few macrolepidopteran caterpillars.
Tomado 226932 (491)	1000	Aug. 1973	On rotting trunk lying across narrow stream in high, primary forest. **Stomach**: partially full of orangish tan soft fruit mash containing masticated remains of a few macrolepidopteran caterpillars, a cockroach, and a small adult beetle.
Gunung Kanino 225501 (2545)	1402	Feb. 1975	On wet, rotting limb lying across small stream (Sungai Salubeka) bordered by dense forest understory in steep canyon. A rat, *Paruromys dominator*, was also trapped here. **Stomach**: packed with large (20–30 mm long) macrolepidopteran caterpillars mixed with a bit of blackish debris clinging to everything; no other kind of insects.
225502 (2547)	1402	Feb. 1975	On large rotting, moss-covered trunk lying across Sungai Salubeka. Stomach empty.
225504 (2487)	1418	Feb. 1975	On rotting, wet, moss-covered tree limb bridging the Sungai Salubeka. **Stomach:** packed with a mass of small (10–15 mm long) macrolepidopteran caterpillars, whole and in pieces, mixed with brownish black debris, similar to ASE 2545 except larvae are much smaller.
225503 (2466)	1418	Jan. 1975	On limb growing across Sungai Salubeka in canyon. **Stomach**: half full with dark brown and tan remains of fruit, along with chewed pieces of several macrolepidopteran caterpillars, and bits of a small adult beetle.
223532 (829) 223533 (831)	1463	Nov. 1973	On rotting trunk lying along ground in forest. **Stomach of 829**: full of orange-brown soft fruit mash (same stuff as in 831 and other squirrels from Gunung Kanino) and remains of two macrolepidopteran caterpillars. **Stomach of ASE 831**: distended with orange-brown soft fruit mash mixed with the masticated remains of a few macrolepidopteran caterpillars, and several cockroaches.
223534 (845)	1463	Nov. 1973	On wet, rotting tree trunk lying on ground in forest. **Stomach**: nearly empty except for a few bits of soft fruit (mostly rind) and remains of two macrolepidopteran larvae (caterpillars).

TABLE 32
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
223535 (854)	1463	Nov. 1973	On wet, rotting, moss-covered trunk lying across Sungai Salubeka near camp. **Stomach**: bits of soft fruit (skin and pulp), large and black hard pyramidal seeds; remains of two macrolepidopteran caterpillars, and a few small adult beetles.
225505 (3017)	1509	May 1975	On decaying trunk (6 in. diameter, top clear, sides mossy) lying across stream extending from one terrace to the opposite terrace and 5 ft above water surface. A *Prosciurillus murinus* was trapped at same spot on a different day. **Stomach**: full of soft fruit mash.
225506 (3037)	1540	May 1975	On rotting, moss-covered trunk lying across wet ravine 8 ft above stream, hillside forest.
225507 (3052)	1540	May 1975	On moss-covered branch bridging ravine 6 ft above surface of water.
Gunung Nokilalaki 223531 (1144)	2293	Dec. 1973	Shot out of short, moss-covered tree on summit. **Stomach**: mostly full of tannish orange soft fruit mash; also contains remains of a few small legless beetle larvae, some small adult beetles, and a cockroach.

(Siphonaptera, Leptopsyllidae) is recorded from a voucher host collected at Tomado, and the same species of flea also parasitizes five species of endemic Sulawesian murid rodents: *Bunomys fratrorum*, *B. penitus*, *Eropeplus canus*, *Maxomys musschenbroekii*, and *Paruromys dominator* (Durden and Beaucournu, 2000). Murids are typical hosts of *Sigmactenus* spp. fleas (Durden and Traub, 1990) so the record of *S. sulawesiensis* from *P. topapuensis* is likely an atypical host association (Durden and Beaucournu, 2000). *Farhangia sedecimdentata* (Pygiopsyllidae) was found on voucher squirrels collected at Sungai Tokararu and Gunung Kanino, and to date has not been discovered parasitizing other rodents (Mardon and Durden, 2003). The squirrel hosts were initially identified as *Prosciurillus leucomus*. *Farhangia* spp. are considered to be "nest fleas" of Asian (Bornean and Sulawesian) tree squirrels (Traub, 1980); *F. sedecimdentata* is therefore probably more common in nests of *P. topapuensis*.

SYMPATRY: The range of *P. topapuensis* in the central core of mainland Sulawesi overlaps those of the tree squirrels *P. murinus*, *Rubrisciurus rubriventer*, and both species of ground squirrels, *Hyosciurus* (table 6). Along his transect in the northern portion of central Sulawesi, Musser caught *P. topapuensis* in the same traplines along with examples of those four species, and sometimes in the same traps (see table 32).

SYNONYMS: Only one scientific name is a synonym of *P. topapuensis*: reasons behind its allocation are presented below.

Callosciurus leucomus hirsutus Hayman 1945: 576. HOLOTYPE: BMNH 40.691g (stuffed museum study skin and slightly damaged skull; see table 13 for measurements), an adult male collected by W.J.C. Frost in 1938 or 1939. TYPE LOCALITY: Tamalanti, a "Plantation between Rantekaroa [02°50′S, 119°50′E] and Koelawi [01°27′S, 119°59′E]" (Laurie and Hill, 1954: 156), 3300 ft (1006 m), in the western portion of the central core of the island, Propinsi Sulawesi Selatan, Indonesia.

Frost collected six tree squirrels from Tamalanti, and Hayman (1945: 577) considered them to represent a member of the "peculiar *leucomus* group" and diagnosed *Callosciurus leucomus hirsutus* this way:

> Slightly smaller, according to available skull measurements, than typical *leucomus*; general

colour above, a uniform warm grizzled mixture of amber- brown and black, below, pale buffish mixed with grey, the buff colouring most clear and intense on throat and chest. The underside very distinct from the clear brick red of *leucomus* and other related forms, but sharing this distinction with *Callosciurus topapuensis* Roux (the nearest form geographically). Ears clothed above with black hairs, forming a distinct tuft contrasting with the colour of head and body. Tail short, of same general hue as body, but with long terminal pencil or tuft of all black hairs. Coat very full and shaggy.

"The shaggy coat is particularly long and full in [*hirsutus*]" wrote Hayman (1945: 578), "and in conjunction with the tufted ears and particularly long terminal tail tuft suggested the subspecific name." While Hayman appreciated the unique coloration of the fur characterizing *hirsutus*, he did not consider it to be diagnostic of a separate species; "*Callosciurus leucomus hirsutus* is strikingly different from *C. leucomus leucomus* of N. E. Celebes in colour, but is here treated as a subspecies to indicate relationship, in view of its obvious affinities as shown by the skull" (Hayman, 1945: 578). Hayman acknowledged that among the named forms of *Callosciurus leucomus* (mentioning *leucomus* and *occidentalis* but not *alstoni*, *tonkeanus*, *sarasinorum*, *mowewensis*, or *elbertae*), *hirsutus* resembled only Roux's (1910) *Callosciurus topapuensis*, which he knew only from Roux's published description, writing "But *topapuensis* is said to have ear tufts coloured as the head, and to have the sides of the body, and the limbs a lighter, more yellowish, tone than the back, two characters which definitely do not apply to the Tamalanti form." But these tonal aspects of Roux's description do apply to all six of Hayman's *hirsutus*. In these and all examples of the other species in the *Prosciurillus leucomus* group, sides of the body and dorsal surfaces of the limbs and feet are slightly paler than the back due to the pale buff or cream bands on the overhairs in the fur covering these regions, as we explained above. The contrast in color of the ear tufts, from concolorous with the head, as in the holotype of *topapuensis*, to black as described by Hayman for *hirsutus* reflects extremes in the range of variation we see within our sample from several highland regions in the central core of Sulawesi.

Some dimensions of the skull from the holotype of *hirsutus* (kindly measured for us by Paula Jenkins) are slightly smaller than those for the holotype of *topapuensis* (table 13). This distinction is reflected in the ordination of specimen scores projected onto first and second principal components derived from principal-components analysis that is shown in figure 26B where the score for *hirsutus* falls among scores representing specimens from Rano Rano, Gunung Lehio, Besoa, and Pegunungan Latimojong. Mean values for cranial dimensions average smaller in these highland samples than in the material from Sungai Miu and Sungai Sadaunta, which is closer to the holotype of *topapuensis* in size of skull. Again, the two holotypes represent variation within a single species, this time in cranial dimensions, with the skull of *hirsutus* nesting with the smaller specimens and that of *topapuensis* with the larger individuals (fig. 26B, table 30).

Prosciurillus rosenbergii (Jentink, 1879)

Sciurus Rosenbergii Jentink, 1879: 37.
Sciurus tingahi Meyer, 1896: 27.

LECTOTYPE AND TYPE LOCALITY: The lectotype of *Prosciurillus rosenbergii* is a young adult female (RMNH 13362, specimen "l" in Jentink's [1888: 24] catalog) obtained by D. Hoedt on October 27, 1865, from "Siao," Kepulauan Sangihe. It consists of a skin mounted in a live pose and an incomplete skull (extracted from the mount after Jentink's tenure at Leiden). Values from dental and some cranial measurements are listed in table 14.

Specimen "l" was one of 12 specimens cataloged as "types" (= syntypes) by Jentink (1887: 190–191, 1888: 23–24). All the skulls are badly damaged or smashed. At the suggestion of Chris Smeenk (in litt., 2008), we select specimen "l" as lectotype following the procedure stipulated in Article 74.1 of the Code; ICZN, 1999: 82). Of the 12 syntypes, specimen "l" "has a beautiful skin and the second best skull" (C. Smeenk, in litt., 2008). The remaining 11 specimens become paralectotypes: **(1)** specimen "*a*" (Jentink,1888: 23), RMNH 13351, a mounted skin and

incomplete skull, male, from "Sanghi" (= Pulau Sangihe or Kepulauan Sangihe), collected November 7, 1864, by collectors for C.B.H. von Rosenberg; **(2)** specimen "*b*" (Jentink, 1888: 23), RMNH 13352, a mounted skin and cranial fragments, female, from "Sanghi" (= Pulau Sangihe or Kepulauan Sangihe), collected November 2, 1864, by collectors for C.B.H. von Rosenberg; **(3)** specimen "*c*" (Jentink, 1888: 23), RMNH 13353, a mounted skin and incomplete skull, female, from "Sanghi" (= Pulau Sangihe or Kepulauan Sangihe), collected November 10, 1864, by collectors for C.B.H. von Rosenberg; **(4)** specimens "*a*" (the skull, in Jentink's osteological catalog, 1887: 190) and "*d*" (the skin, in Jentink, 1888: 24), RMNH 13354, a mounted skin and incomplete skull, male, from "Sanghi" (= Pulau Sangihe) collected January 16, 1866, by D. Hoedt; **(5)** specimen "*e*," RMNH 13355, a mounted skin and incomplete skull, male, from "Siao" (= Pulau Siau) collected October 20, 1865, by D. Hoedt; **(6)** specimens "*b*" (the skull, in Jentink, 1887: 190) and "*f*" (the skin, in Jentink, 1888: 24), RMNH 13356, a mounted skin and incomplete skull, male, from "Siao" (= Pulau Siau) collected October 23, 1865 by D. Hoedt; **(7)**; specimen "*g*" (Jentink, 1888: 24), RMNH 13357, a mounted skin and fragments of a skull, male, from "Siao" (= Pulau Siau) collected October 22, 1865 by D. Hoedt; **(8)** specimens "*c*" (the skull, in Jentink, 1887: 190) and "*h*" (the skin, in Jentink, 1888: 24), RMNH 13358, a mounted skin with incomplete skull, male, from "Siao" (= Pulau Siau) collected October 24, 1865, by D. Hoedt; **(9)** specimen "*i*" (Jentink, 1888: 24), RMNH 13359, a mounted skin along with skull fragments, male, from "Siao" (= Pulau Siau) collected October 24, 1865, by D. Hoedt; **(10)** specimens "*d*" (the skull, in Jentink, 1887: 192) and "*j*" (the skin, in Jentink, 1888: 24), RMNH 13360, mounted skin and damaged skull, male, from "Siao" (= Pulau Siau) collected November 9, 1865, by D. Hoedt; **(11)** specimens "*e*" (the skull, in Jentink, 1887: 192) and "*k*" (the skin, in Jentink, 1888: 24), RMNH 13361, a mounted skin and partial skull, female, from "Siao" (= Pulau Siau) collected October 23, 1865, by D. Hoedt. Skulls "*a–e*," were removed during Jentink's tenure; the others were extracted later.

The type locality is Kepulauan Sangihe, Pulau Siau (also spelled "Siao"), 02°49′N, 125°23′E (see gazetteer and map in figure 28), Propinsi Sulawesi Utara, Indonesia. No details are recorded concerning the precise collection locality on Pulau Siau.

Chris Smeenk (in his manuscript pages of the "Type-specimens of recent mammals in the National Museum of Natural History, Leiden"; sent to us in 2009) notes that "Jentink (1888) omitted the locality for the specimens collected by von Rosenberg. The latter did not visit the Sangir islands himself, but had sent local hunters to collect on the islands during the period September–November 1864; see his notes preserved in the archives of the Leiden Museum. It is not recorded on which island the material was collected."

EMENDED DIAGNOSIS: *Prosciurillus rosenbergii* is comparable in body size and length of tail relative to head and body length to other species in the *P. leucomus* group (tables 14, 15). It is unique among members of that cluster by having dark brown or chestnut brown upperparts without contrasting chromatic patterns (no patches on the nape behind the ears, no black middorsal stripe) or adornments (no ear tufts), dark brownish gray or brownish buff underparts (no specimen with reddish-orange to ochraceous or dark gray ventral fur) and blackish tail.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: *Prosciurillus rosenbergii* is endemic to Kepulauan Sangihe where samples come from Pulau Sangihe, the largest island in the archipelago; the smaller Pulau Siau, south of Sangihe; and the small islands of Tahulandang and nearby Ruang (see table 4 and fig. 28). All the specimens were collected during the latter 1800s and none have information indicating elevations at which they were caught. We do not know the present status of the species in the archipelago but would not be surprised if most populations are extinct. Whitten et al. (1987: 49) write that "Virtually all of [Pulau] Sangihe has been converted to coconut and nutmeg plantations or else is covered in patches of secondary forest from abandoned gardens," and that "Sangihe and other northern islands were largely deforested by 1920" (p. 91).

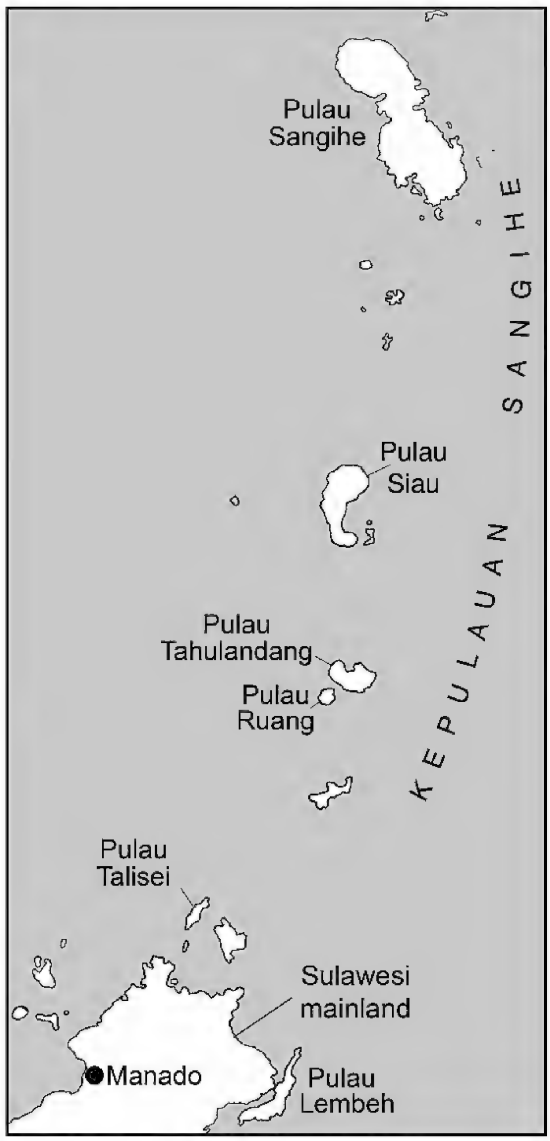

Fig. 28. Collection localities for samples of *Prosciurillus rosenbergii* in the Sangihe Archipelago (Kepulauan Sangihe) north of mainland Sulawesi's northeastern tip. Samples come from Pulau Sangihe, Pulau Siau, and Pulau Tahulandang and the nearby Pulau Ruang. *Prosciurillus rosenbergii* is the only squirrel ever collected in this group of islands and occurs nowhere else. To the south, off the northeastern tip of Sulawesi's northern peninsula, *P. murinus*, which is found throughout the mainland, has been collected on Pulau Talisei and Pulau Lembeh, and *P. leucomus*, ranging over the northern peninsula, is recorded from P. Lembeh (see gazetteers for these two species).

Two other species of nonvolant mammals are endemic to the Sangihe Archipelago, both recorded only from Pulau Sangihe. One is the primate, *Tarsius sangirensis*, which is very different in its morphology compared with samples of tarsiers from mainland Sulawesi and adjacent islands (Feiler, 1990; Groves, 2005). The other is a distinctive species of murid rodent related to those in the *Rattus xanthurus* group on mainland Sulawesi and nearby Pulau Peleng (Musser, MS; Musser and Carleton, 2005: 1462).

The islands forming Kepulauan Sangihe are mostly volcanos ringed by coastal lowlands scattered along the wide volcanic Sangihe arc platform, most of which is submerged about 1000 m beneath sea level (Sheets NA 51-4 and 51-12). Volcanic activity along the arc has been present since middle Miocene times (Hall, 2002: 382). Pulau Biaro, the southernmost island in the archipelago, is separated from Pulau Talise and Pulau Bangka, lying just off the Sulawesi mainland in shallow water, by sea at least 1000 m deep. There is no current evidence of any past Pleistocene or earlier land connection between the archipelago and mainland; presumably the ancestors of the few nonvolant mammals restricted to the archipelago reached the islands by some form of overwater dispersal.

DESCRIPTION: The highlights of Jentink's (1879: 37) description portray a squirrel characterized by coloration of fur strikingly different from any members of the *P. leucomus* group occurring on mainland Sulawesi and closely adjacent offshore islands.

> General tint of the upperparts of the body and outside of legs rusty brown; the colour of the underparts is much brighter. Hairs of the back with a broad black ring towards the tip. Tail darker than the back, each long hair is embellished with a broad black ring and a very long black tip. In-and outside of the ears closely covered with hairs which do not form a pencil. Whiskers black and not projecting beyond the tips of the ears. Toes and fingers and also the fore and hind-feet closely covered with hairs on the upper parts, the hairs being here dusky near the base with silvery tips.

Prosciurillus rosenbergii is comparable to squirrels in samples of *P. leucomus*, the

member of the *P. leucomus* group that is closest geographicallyto *P. rosenbergii*, in size of body, appendages, and length of tail relative to head and body length (table 15), but strikingly different in coloration of pelage and without any of the color patterns seen in the other members of the *P. leucomus* complex. The entire upperparts—head, neck, back, ears, and dorsal surfaces of the feet—of specimens from the two northern islands, Sangihe and Siau, are rich chestnut-brown (Jentink's "rusty brown"), a background due to the mix of dark gray underfur, longer overhairs that are dark gray for most of their length and tipped with subterminal reddish brown and black bands, and the glossy dark guard hairs. The dorsal coat is unmarked by ear tufts, nape patches, or a middorsal black stripe. The underparts range from dark brownish gray to brownish buff and hardly contrast with color of the fur over dorsal surfaces of the head and body; hairs are dark gray basally and tipped with brown or brownish buff bands. Squirrels in samples from the southern island, Tahulandang, and its nearby smaller companion, Ruang, are slightly paler, having brown upperparts and brownish buff underparts. In all samples, the tail conspicuously contrasts with the head and body because it is blackish with rusty highlights everywhere, an effect resulting from the long black hairs with subterminal dark brown bands and long black tips (as Jentink observed, "each long hair is embellished with a broad black ring and a very long black tip." See Feiler's (1990: 89) black and white images of *P. rosenbergii* and Meyer's [1896] color plate, which is reproduced in figure 9.

Females exhibit three pairs of teats, one postaxillary pair and two inguinal pairs.

Although all the skulls we examined are damaged in some way, the intact portions are closely similar to comparable cranial sections in skulls of other species in the *P. leucomus* group; cranial and dental measurements for some dimensions are summarized in table 17.

COMPARISONS: Brown or chestnut-brown upperparts, slightly paler underparts, and a blackish tail define the color pattern peculiar to *P. rosenbergii*. All other species in the *P. leucomus* group have brown upperparts flecked with orange and buff, and the underparts are reddish orange to ochraceous (*P. leucomus*), reddish brown to reddish orange (*P. alstoni* and *P. weberi*), or dark gray with a silver or buffy wash (*P. topapuensis*). The ears are the same color as the head and neck and lack tufts (conspicuous black tufts in *P. leucomus*, *P. topapuensis*, and *P. weberi*; white tufts in *P. alstoni*), no white, buffy or gray patches adorn sides of the neck behind the ears (nape patches are typical in *P. leucomus*) and no middorsal black stripe marks the back (diagnostic for *P. weberi*). The tail is blackish flecked with rust except at the tip (the tail is the same color as upperparts in the other species and only the long tuft at the end is black). Because all the skulls available for measuring are severely damaged, we cannot provide comparative morphometric analyses other than to report that mean values of those dimensions that could be measured are comparable to those derived from samples of other species in the *P. leucomus* group (table 17).

GEOGRAPHIC VARIATION: Other than the slight difference in color saturation of the pelage in samples from the two northern islands in the Archipelago as opposed to the southern Pulau Tahulandang and neighboring Pulau Ruang, we can provide no information on aspects of other kinds of variation that might be associated with island location. Insular variation in cranial and dental dimensions among samples from the four islands cannot be assessed because all skulls are incomplete.

ECOLOGY: No information is available. In its morphology, *P. rosenbergii* is closely related to other members of the *P. leucomus* group, and we suspect the species to inhabit primarily the upper canopy as Musser observed for *P. alstoni* and *P. topapuensis*; only direct field observations will provide this kind of information.

ECTOPARASITES: No records. Durden combed the fur in a large sample of *P. rosenbergii* but could not locate any attached sucking lice.

SYMPATRY: No other species of squirrel has ever been collected on any island in Kepulauan Sangihe.

SYNONYMS: The only other scientific name attached to *Prosciurillus rosenbergii* is discussed below.

Sciurus tingahi Meyer, 1896: 27. LECTOTYPE: SNSD B2842 (stuffed museum study skin and damaged skull; see table 14 for measurements), an adult male purchased from Charles Cursham in 1894. TYPE LOCALITY: Kepulauan Sangihe, Pulau Tahulandang, 02°21′N, 125°25′E, Propinsi Sulawesi Utara, Indonesia (see gazetteer and map in figure 28). No details are recorded about the precise collection locality on Pulau Tahulandang.

Feiler (1999: 408–409) identified SNSD B2842 as the "holotype" and four other specimens as paratypes. Meyer (1896: 27) based his description of *tingahi* on several specimens without identifying a holotype so the specimen Feiler set aside as holotype is a lectotype and the others are paralectotypes (see Article 74.5 of the Code [ICZN, 1999: 82–83], and our accounts of *P. leucomus* and *P. alstoni*).

Although described as a separate species related to *Prosciurillus rosenbergii* from the northern Pulau Sangihe and Pulau Siau, we consider Meyer's sample of *tingahi* to represent populations of *P. rosenbergii* on the southern Pulau Tahulandang and closely adjacent Pulau Ruang. Specimens of *tingahi* have slightly paler pelage than those from Pulau Sangihe and Pulau Siau, brown upperparts and buffy brown underparts as opposed to dark chestnut brown upperparts and dark brownish gray or buff venters in squirrels from the two northern islands. Meyer's *tingahi* is portrayed in his color plate reproduced in figure 9.

Prosciurillus sp.

A fragment of a right dentary (fig. 29) from an adult squirrel was found in sediments excavated from Ulu Leang I, a cave about 40 km northeast of Ujung Pandang in the Maros region near the tip of Sulawesi's southwestern peninsula (see gazetteer and fig. 11). Excavations in the cave were described by Glover (1976), who also provided us with 10,000–3500 years B.P. as a rough interval of the dated sediments (Glover, in litt., 1989). A more precise date associated with the particular site ("Trench J") at which the piece was uncovered is unavailable.

The size of the subfossil fragment (the body of the dentary) matches dimensions of the dentaries in members of the *Prosciurillus leucomus* group and not the two species in the much smaller-bodied *P. murinus* group (see fig. 29 where the subfossil is compared with a modern member of each group, and table 33 for comparative measurement values). No modern representatives of the *P. leucomus* group have been collected from Sulawesi's southwestern peninsula. The sample of *P. weberi* from Masamba and Palopo on the coastal plain in the far southeastern lowlands of the central core of Sulawesi (see map in fig. 11) is the closest to the provenance of the subfossil. At present we cannot tie the subfossil to *P. weberi*; or to *P. alstoni*, which ranges over the eastern sector of the central core of the island and throughout the southeastern peninsula; or to *P. topapuensis*, which inhabits forests in the foothills and mountains in the western sector of the central core north of the range of *P. weberi* (see map in fig. 11); or determine if the subfossil represents a different species restricted to the southwestern peninsula. Dentaries of all these species are closely similar in size and shape, especially the body of the dentary, which is all that remains of the subfossil. Possibly DNA can be extracted from the fragment and compared with samples taken from specimens of the modern species to resolve the issue.

Modern specimens of the small-bodied *P. murinus* have been collected on the flanks of Gunung Lompobatang at the tip of the southwestern peninsula (see gazetteer and fig. 30). The squirrel likely inhabited lowland forest in the Maros region before the landscape was transformed from forest to agricultural plains and may have been sympatric with *Prosciurillus* sp. during the 10,000–3,500-year interval. The large-bodied *Rubrisciurus rubriventer* also once occurred on the peninsula, documented by a subfossil cranial fragment (see account of *R. rubriventer*).

Archaeological remains of squirrels from caves at the tip of Sulawesi's southwestern peninsula are extremely rare. Of the more than 1000 specimens of mammals excavated from cave sites at the southern end of the southwestern peninsula during the 1900s (see

Fig. 29. Subfossil fragment from a right dentary of *Prosciurillus* sp. (AMNH 269955) from Ulu Leang I, a cave about 40 km northeast of Ujung Pandang in the Maros region near the tip of Sulawesi's southwestern peninsula. Size of the fragment fits with dentaries typical of species in the *Prosciurillus leucomus* group, which in this figure is represented by *P. alstoni* (bottom labial and lingual views, AMNH 101331) from Wawo in the southeastern peninsula (see gazetteer and fig. 11 for *Prosciurillus* sp. and *P. alstoni*), and not the smaller-bodied *P. murinus* (top set, AMNH 101388), represented here by a sample from Lombasang on the flank of Gunung Lompobatang, east of the Maros region on the southwestern peninsula (see gazetteer and map in fig. 30 for *P. murinus*). All views are ×2. Additional information is presented in the text and table 33.

Dammerman, 1939; Hooijer, 1950; Clason, 1976; Musser, 1984; Simons, 1997), only three squirrels have been noted. One was described by Sarasin (1905) as "*Sciurus rubriventer*?," a cranial fragment excavated from cave sediments along with skeletal pieces of other mammalian species. The other two were excavated from sediments in Ulu Leang I, the dentary fragment of *Prosciurillus* we describe here and a "maxilla" listed in a table by Clason (1976: 66); she provided no details. We have not seen Sarasin's specimen, but his account clearly describes a *Rubrisciurus rubriventer*. Clason's material was excavated by Glover from Ulu Leang I mostly during 1973. We do not have access to those specimens. Our dentary fragment was found during Glover's 1975 excavation of the cave and sent to Musser along with other mammalian fragments.

Clason (1976: 66) tabulated more than 1000 mammalian cranial and postcranial fragments found by Glover in Ulu Leang I (no estimate of the actual number of individuals represented is available). Some were not yet identified at the time of her report, but 852 were given preliminary identifications. Of these, one represents a squirrel, 65 are from non-sciurid rodents, and the rest sample phalangers, bats, primates, carnivores, and artiodactyls. Non-sciurid rodents, especially those of large body size such as the species of *Lenomys*, *Paruromys*, and *Taeromys* are hunted today in other parts of Sulawesi; drift fences made of palm fronds are used with snares placed in openings along the drift

TABLE 33
Measurements (mm) of Alveolar Lengths of Molar Rows (ALpm4–m3) in Dentaries from Samples of a Subfossil and Modern *Prosciurillus*[a]
Mean ± 1 SD and observed range (in parentheses) are listed for the extant specimens, which are identified in footnotes.

Locality and specimen	*N*	ALpm4–m3
P. sp. (subfossil)		
Southwestern peninsula, Ulu Leang I[b]	1	7.9
P. weberi (modern)		
Southwestern peninsula[c]	4	7.9 ± 0.08 (7.8–8.0)
P. alstoni (modern)		
Southeastern peninsula[d]	20	8.1 ± 0.19 (7.8–8.4)
P.murinus (modern)		
Southwestern peninsula[e]	8	6.3 ± 0.12 (6.1–6.5)

[a]The measurements are meant to show that the subfossil fragment is from a member of the *Prosciurillus leucomus* group (of which *P. weberi* and *P. alstoni* are components) and not the smaller-bodied *P. murinus*. *Prosciurillus weberi* occurs in the southern sector of the central core of Sulawesi just north of the southwestern peninsula (see map in fig. 11), and the four specimens included in the table are from a lowland sample of the *P. leucomus* group that is geographically closest to the provenance of the subfossil. The sample of *P. alstoni*, also from the lowlands, comes from the southeastern peninsula just east of the source for the four specimens of *P. weberi*. The only other member of the group occurring in central Sulawesi is *P. topapuensis*, which is found in the mountains and foothills north of *P. weberi*.

[b]Fragment of a right dentary without an incisor, premolars, or molars (AMNH 269955; fig. 29). The alveoli for premolars and molars are intact. The dimension was measured from the anterior alveolar rim for the fourth premolar to the posterior alveolar lip of the third molar (ALpm4–m3).

[c]Masamba: MZB 6252, 6253. Palopo: MZB 6254, 6256.

[d]Wawo: AMNH 101329–37, 101339. Masembo: AMNH 101340–46. Lalolis: AMNH 101326–28.

[e]Gunung Lompobatang, Lombasang: AMNH 101381–89.

fence (Musser's observations in central Sulawesi). Likely some of the rodent fragments from Ulu Leang I represent remnants of prehistoric human meals (see Musser, 1984); other pieces are probably from owl pellets, although some could be from the scat of the endemic Sulawesian civet *Macrogalidia musschenbroekii*. That carnivore may be represented by isolated teeth from Ulu Leang I (Clason, 1976) and skeletal fragments have been collected from other prehistoric cave sediments in the region (Hooijer, 1950). In the upper montane forest on Gunung Nokilalaki, Musser frequently saw *Macrogalidia* and found feces containing cranial and postcranial bits of the murid, *Bunomys penitus*, which is the most common small rodent in that forest.

In contrast to the murid rodents, all the endemic species of Sulawesi squirrels are diurnal and less exposed to owl predation, although some now and again are likely taken by hawks, eagles, and *Macrogalidia*. Squirrels are seen but rarely caught by the local people. According to the villagers Musser encountered in the forest, none had ever caught squirrels in their snares set along drift fences. Rather than running alongside a drift fence as rats do, squirrels would simply bound over it. Rats and mice can also be dug out of their burrows, but getting to nests of tree squirrels is more difficult. The prehistoric people living on the southwestern peninsula may have had equal difficulty in capturing squirrels, or it was simply more efficient in time and energy to hunt and capture larger mammals along with rats and mice.

The *Prosciurillus murinus* Group

Two species comprise this cluster, both the smallest in body size among all the tree squirrels and ground squirrels endemic to Sulawesi. One is *Prosciurillus murinus*, named and described by Müller and Schlegel in

TABLE 34
Allocation of Scientific Names Associated with Species in the *Prosciurillus murinus* Group as Presented in Primary Published Checklists of Mammals from 1940 to the Present
Generic and specific names as originally published are listed in their published chronological order. See the species accounts for names of authors and dates of publication.

Original combination (in *Sciurus*, *Sciurillus*, or *Prosciurillus*)	Ellerman, 1940 (in *Sciurillus*)	Laurie and Hill, 1954 (in *Prosciurillus*)	Corbet and Hill, 1992 (in *Prosciurillus*)	Thorington and Hoffmann, 2005 (in *Prosciurillus*)	Present report (in *Prosciurillus*)
S. murinus	*Sc. murinus murinus*	*P. murinus murinus*	*P. murinus murinus*	*P. murinus murinus*	*P. murinus*
S. murinus necopinus	*Sc. murinus necopinus*	*P. murinus necopinus*	*P. murinus necopinus*	*P. murinus necopinus*	*P. murinus*
S. evidens	*Sc. murinus evidens*	*P. murinus*	*P. murinus evidens*?	*P. murinus evidens*	*P. murinus*
Sc. murinus griseus	—	*P. murinus murinus*	*P. murinus griseus*	*P. murinus griseus*	*P. murinus*
P. abstrusus	—	—	*P. abstrusus*	*P. abstrusus*	*P. abstrusus*

1844, which has been collected from most of mainland Sulawesi where it occurs through an altitudinal gradient from coastal lowlands to mountains and within the range of forest formations from tropical lowland evergreen rain forest to upper montane rain forest; specimens were also taken from two small islands off the northeastern coast of the northern peninsula. The other is *Prosciurillus abstrusus*, named and described by Moore in 1958; it has only been collected at 1500 m and 2000 m in montane forest on Pegunungan Mekongga, the highest range on the southeastern peninsula of Sulawesi.

Although originally described as a species of *Sciurus*, the genus used for most new species of squirrels described during the 1800s and early 1900s, *murinus* was eventually transferred to *Sciurillus* (Ellerman, 1940: 318) then subsequently designated the type-species of *Prosciurillus* (Ellerman, 1947: 259) where it has remained (see table 34 and introduction to *Prosciurillus*).

Three scientific names have been associated with *murinus*, one described as a separate species, the other two as subspecies of *murinus*; after 1947 all were either recognized as subspecies or synonyms (table 34). From our study of skins and skulls, we can delineate a single species, *P. murinus*, and similar kinds of data sources indicate *P. abstrusus* to be a separate but related species. Concordant with the morphological data identifying two distinctive species are their sucking lice parasites: each species of squirrel supports a distinctive species of *Hoplopleura* (see the descriptions of sucking lice).

Definitions of the species limits of *P. murinus* and *P. abstrusus*, based on qualitative evaluation of variation in coat color combined with morphometric analyses of cranial and dental dimensions, along with summaries of their geographic and altitudinal distributions derived from collection localities of voucher specimens, and contrasts between the two, are provided in the following accounts.

GAZETTEER AND SPECIMENS EXAMINED: Collection localities for the 197 specimens of *P. murinus* and the 30 examples of *P. abstrusus* studied are listed below. The number preceding each locality keys to a symgbol on the map in figure 30.

Prosciurillus murinus

1. **Pulau Talise**, 01°50′N, 125°03′E, sea level (highest point on island is 264 m): BMNH 87.7.15.1.
2. **Teteamoet** (several miles southeast of Likupang; see Raven's brief description of the place in Miller, 1917: 29), 01°40′N, 125°05′E (estimated from Raven's map), on coastal plain near sea level: USNM 216793–95.
3. **Manado** (also spelled "Menado"), 01°30′N, 124°50′E, coastal plain near sea level: ANZP 14156; BMNH 88.7.15.1, 97.1.2. 18; MZB 5975, 5978; RMNH 13216–18 (specimens

"*d–f*" in Jentink's [1888: 22] catalog; specimen "*e*" is actually from "Ménado-Langowan).

4. **Gunung Klabat** ("Goenoeng Kalabat" on specimen labels), 01°28′N, 125°02′E: AMNH 196512 ("Koemersot," 250 m on skin label); USNM 217809 (5600 ft [1707 m]). This specimen was collected by H.C. Raven, who provided this note (quoted in Riley, 1924: 1): "My camp was at about 1,700 meters (5,600 feet), where the forest is only semitropical in appearance. Practically all the trees are heavily coated with moss and are not tall. Kalabat is the highest mountain in Minahassa, having an altitude of 2,020 (6,617) feet."
5. **Pulau Lembeh**, 01°26′N, 125°13′E (elevation of collection site is not recorded but highest point of the island is 447 m): BMNH 40.631, 40.632; SNSD 3081; USNM 217810–13, 217814 (holotype of *Sciurus evidens*), 217815.
6. **Rurukan**, 01°21′N, 124°52′E: AMNH 196510 (900 m), 196511 (1000 m); BMNH 97.1.2.17, no elevation is recorded for the specimen, but Rurukan is at 1000 m; Sheet NA 51-12).
7. **Tonsealama** (also known as "Tonsea"), 01°19′N, 124°55′E, 600–700 m (estimated from Sheet NA 51-12): MZB 5976, 5977.
8. **Tomohon**, 01°19′N, 124°49′E, 700–800 m (estimated from Sheet NA 51-12): BMNH 99.10.1.6. Meyer (1898: 21) reported specimens from Tomohon.
9. **Temboan** (on Kuala Kalait, "is a new clearing of eight houses and lies from Mt. Sapoetan south, 55° west and about six miles from Loboe," wrote Raven in his field journal, 1916: 3 (in mammal division library, USNM), 01°03′N, 124°33′E (estimated from Raven's map), 500 m (estimated from Sheet NA 51-12): USNM 217816–21.
10. **Amurang**, 01°11′N, 124°35′E, on coastal plain near sea level: MZB 1502–1505.
11. **Pinogu, Bone Valley** (also spelled Pinogoe), 00°32′N, 123°25′E, 200 m (estimated from Sheet NA 51-14): BMNH 99.10.1.23.
12. **Gorontalo**, 00°31′N, 123°03′E, coastal plain near sea level: RMNH 13215 (specimen "*c*" in Jentink's [1888: 22] catalog).
13. **Bumbulan**, 00°29′N, 122°04′E, coastal plain near sea level: AMNH 152921, 152932, 152938–43, 153281, 153282; MZB 5973; RMNH 9827 (formerly MZB 5974; holotype of *Sciurillus murinus griseus*).
14. **Sungai Paleleh** ("I went inland about four or five miles over the mountains and made camp at the edge of the Paleleh River, which is a small brook ... with steep mountains or hills on all sides" [Raven, in Miller, 1915: 23]), 00°59′N, 121°49′E (estimated from Raven's map), 700 m (estimated from Sheet NA 51-14): USNM 200275–78.
15. **Matinan** (also spelled Matinang), 01°05′N, 121°42′E (for village near coast; specimens came from highlands south of village in foothills of Pegunungan Peleleh at 600 m): AMNH 196513–19. Meyer (1898: 21) reported a specimen from "Matinangkette" (Matinan range, part of the larger Pegunungan Peleleh) at 1000 m.
16. **Gunung Ile-Ile**, 00°58′N, 121°48′E (part of the larger Pegunungan Peleleh forming the mountainous backbone of the northwestern portion of the northern peninsula): AMNH 196524–28 (500 m), 196520–23 (1700 m).
17. Valley of Sungai Miu, **Sungai Oha Kecil** (small tributary on left side of Sungai Miu), 01°22′S, 119°57′E (near confluence with Sungai Miu; estimated from Sheet SA 50-8), 290 m: AMNH 224589–91.
18. **Sungai Oha Kecil**, 1300 ft (396 m): AMNH 224592.
19. **Sungai Oha Kecil**, 1400 ft (427 m): AMNH 224593.
20. **Sungai Oha Kecil**, 1600 ft (488 m): AMNH 224594, 224595.
21. Valley of Sungai Miu, **Sungai Miu** (right side), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 350 m: AMNH 224046–49.
22. Valley of Sungai Miu, **Sungai Sadaunta** (also spelled "Sidaonta" or "Sidaunta"; tributary on right side of Sungai Miu), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 675 m: AMNH 224043–45.
23. **Sungai Sadaunta**, 2500 ft (762 m): AMNH 224601–603; 2550 ft (777 m), AMNH 224604.
24. **Sungai Sadaunta**, 2700 ft (823 m): AMNH 224596, 224597, 224605–607.
25. **Sungai Sadaunta**: 2800 ft (854 m), AMNH 224598, 224608, 224609; 2850 ft (869 m), AMNH 224610.
26. **Sungai Sadaunta**: 2900 ft (884 m), AMNH 224599, 224611.
27. **Sungai Sadaunta**: 3000 ft (915 m), AMNH 224600, 224612, 224613; 3050 ft (930 m), AMNH 226836.
28. **Sungai Sadaunta**, 3200 ft (976 m), AMNH 224614, 226837; 3250 ft (991 m), AMNH 224615.
29. **Sungai Sadaunta**, 3300 ft (1006 m): AMNH 224616.
30. **Sungai Sadaunta**, 3400 ft (1037 m): AMNH 224617.
31. Valley of Danau Lindu, **Tomado** (a village on western shore of Danau Lindu), 01°19′S, 120°03′E (estimated from Sheet SA 50-8),

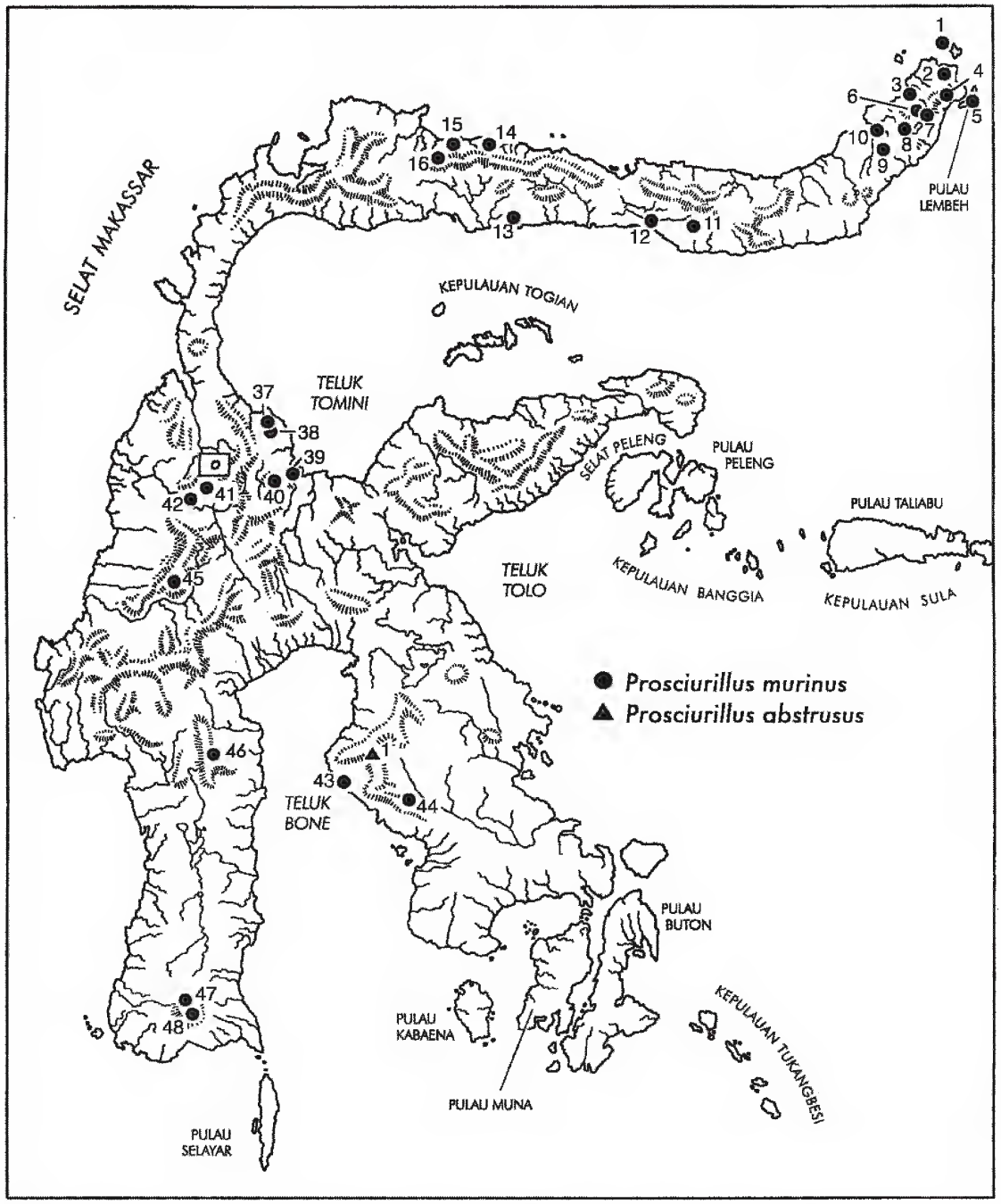

Fig. 30. Collection localities for samples of *Prosciurillus murinus* and *P. abstrusus*. Numbers key to localities described in the gazetteer where specimens are identified by museum initials and catalog numbers. The inset map, right (rectangle in larger map, above), contains collection localities (17–36) for *P. murinus*, which are scattered along Musser's transect from the Sungai Oha Kecil to the higher ramparts of Gunung Nokilalaki. The dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and tropical lower montane forest.

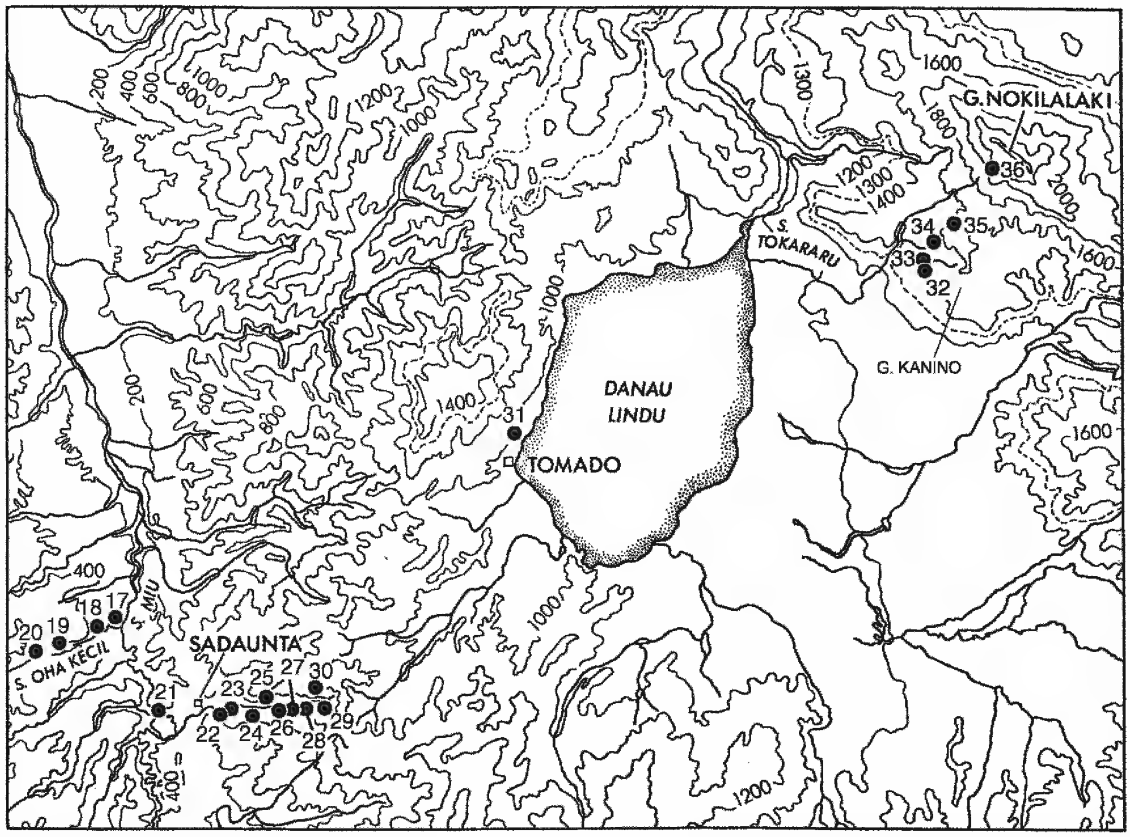

Fig. 30. *Continued.*

1000 m: AMNH 223021, 223022, 223475, 224050, 224051.

32. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 4600 ft (1402 m): AMNH 225492; 4650 ft (1418 m), AMNH 225493–96.
33. **Gunung Kanino**, 4750 ft (1448 m): AMNH 225499; 4800 ft (1463 m), AMNH 223536, 223538, 223539.
34. **Gunung Kanino**, 4900 ft (1494 m), AMNH 225500.
35. **Gunung Kanino**, 5200 ft (1585 m): AMNH 223537.
36. **Gunung Nokilalaki**, 01°13′S, 120°08′E, 7000 ft (2134 m): AMNH 225497; 7100 ft (2187 m), AMNH 223498.
37. Malakosa, **Kuala Navusu**, 00°58′S, 120°27′E (estimated from Sheet SA 51-1): 100 ft (30 m), AMNH 226063–66; 125 ft (38 m), AMNH 226067, 226068; 150 ft (46 m), AMNH 226069; 180 ft (55 m), AMNH 226070; 200 ft (61 m), AMNH 225909; 350 ft (107 m), AMNH 226071; 450 ft (139 m), AMNH 226072, 226073; 600 ft (182 m), AMNH 226074; 750 ft (229 m), AMNH 226075.
38. Tolai, **Sungai Tolewonu**, 01°04′S, 120°27′E (estimated from Sheet SA 50-8): 500 ft (152 m), AMNH 226500–502; 540 ft (166 m), ASE 4174; 600 ft (183 m), AMNH 226503, 226504; 650 ft (198 m), AMNH 226505; 700 ft (213 m), AMNH 226506; 750 ft (229 m), AMNH 226507; 800 ft (244 m), AMNH 226508; 1000 ft (305 m), AMNH 226509.
39. **Pinedapa**, 01°25′S, 120°35′E (estimated from Raven's map), 100 ft (31 m): USNM 219504–507, 219509.
40. **Rano Rano** 01°30′S, 120°28′E, 6000 ft (1829 m): USNM 219508, 219510.
41. **Kulawi**, 01°27′S, 119°59′E, 500 m: USNM 218713.
42. **Gunung Lehio**, 01°33′S, 119°53′E, above 6000 ft (1829 m): USNM 218712 (holotype of *Sciurus murinus necopinus*).
43. **Wawo**, on the plain between the coast and western foothills of Pegunungan Mekongga (also spelled "Mengkoka"), 03°41′S, 121°02′E, 50 m: AMNH 101390–93.

44. Pegunungan Mekongga, **Masembo**, which is southeast of Wawo and the highest place in the southern portion of Pegunungan Mekongga (see maps and discussion in Heinrich [1932] and Stresemann [1940]) 03°35′S, 121°15′E (for the Pegunungan), 550 m: AMNH 101379, 101394.
45. **Pegunungan Takolekaju** ("Molengraff Range," the old the European name for the mountains, is notated on the specimen tags; no more precise collection locality is available; P. Jenkins, in litt., 2008), an extensive mountainous region in the western portion of the central core with the north-south boundaries between approximately 01° and 02°15′S, and extending slightly diagonally from about 119°45′E in the north to 120° near its southern ramparts: BMNH 40.636 (1500 ft, 457 m), 40.365 (3200 ft, 976 m), and 40.367 (3500 ft, 1067 m).
46. **Pegunungan Latimojong**, 03°30′S, 121°23′E, 2200 m: AMNH 196529–33.
47. **Lombasang** (also spelled "Lambasang"), northwest of Gunung Lompobatang, 05°16′S, 119°50′E, 1100 m: AMNH 101380–84, 101387–89.
48. **Gunung Lompobatang** (also spelled Lompobattang; see Fraser and Henson, 1996, for example; spelled "Pik v. Bonthain" or "Pik v. Bantaeng" on old maps), **Wawokaraeng**, 05°20′S, 119°55′E: 2000 m, AMNH 101385, 101386. **Tasoso** (spelled "Dasoso" on the skin tag; a village on the lower slopes and one of Alfred Everett's collection localities [see Hartert, 1896]); 05°17′S, 119°58′E, 4000 ft (1320 m): BMNH 97.1.3.9.

The following specimens were studied but the places where they were caught have not been mapped.

A. **"Nord de Célèbes"**: RMNH 13213 (specimen "*a*" in Jentink's [1887: 190, 1888: 22] catalog), lectotype of *Sciurus murinus* (see account of *P. murinus*). Sody (1949: 77) restricted the type locality to "the extreme N.E. part of the island." **"NE Celebes"**: RMNH 13214 (specimen "*b*" in Jentink's [1888: 22] catalog), paralectotype of *Sciurus murinus*; RMNH 13219 (skull "*c*" in Jentink's [1887: 190] osteological catalog), paralectotype of *Sciurus murinus*. **"Celebes"**: NMB 1172.
B. Northeast peninsula, **Minahasa District** (Kabupaten Minahasa, between 1° and 2° north latitude): BMNH 40.633, 40.634; RMNH 24435, 24436; ZMB 92611–13.
C. Central core, **Tamalanti:** BMNH 40.639, 40.640 (3300 ft, 1006 m); 40.641 (3800 ft, 1159 m). Laurie and Hill (1954: 156) noted that Tamalanti is a "Plantation between Rantekaroa [02°50′S, 119°50′E] and Koelawi [01°27′S, 119°59′E]," which was also the only information Musser and Paula Jenkins found when they searched through field-notes and other documents at BMNH.

Prosciurillus abstrusus

1. Pegunungan Mekongga (also spelled "Mengkoka"), **Tanke Salokko** (the highest spot in Pegunungan Mekongga; see the maps and discussions in Heinrich [1932] and Stresemann [1940]), 03°35′S, 121°15′E (for the Pegunungan): 1500 m, AMNH 101350, 101351; 2000 m, AMNH 101349, 101352–77, 101378 (holotype of *Prosciurillus abstrusus*).

Prosciurillus murinus
(Müller and Schlegel, 1844)

Sciurus murinus Müller and Schlegel, 1844: 87.
Sciurus murinus necopinus Miller and Hollister, 1921: 98.
Sciurus evidens Miller and Hollister, 1921: 99.
Sciurillus murinus griseus Sody, 1949: 77.

Lectotype and Type Locality: The lectotype of *Prosciurillus murinus* is an adult female (RMNH 13213, specimen "*a*" in Jentink's [1888: 22] catalog) obtained by E.A. Forsten sometime during 1840–1842. It consists of a skin mounted in a live pose and a damaged cranium, the latter also listed as specimen "*a*" in Jentink's (1887: 190) osteological catalog. The right zygomatic region is missing, the basicranial area is fragmented, the right bullar capsule is gone, and the cranium is cracked in several other places; both dentaries are missing. Values from dental and some cranial measurements are listed in table 35.

Specimen "*a*" was one of three specimens cataloged as types (= syntypes) by Jentink (1887: 190, 1888: 22). At Chris Smeenk's suggestion (in litt., 2008), we select specimen "*a*" as the lectotype following the rules promulgated in Article 74.1 of the Code (ICZN, 1999: 82); G.H.H. Tate had scribbled "lectotype" on the specimen tag during his visit to Leiden in 1951 (C. Smeenk, in litt., 2008). The other two specimens, collected by E.A. Forsten between 1840 and 1842, become paralectotypes: specimen "*b*" (Jentink, 1888: 22), RMNH 13214, is an adult male skin mounted in live pose with skull still inside the

TABLE 35
Age, Sex, and External, Cranial, and Dental Measurements (mm) for Types of *Prosciurillus murinus* (includes *necopinus* and *evidens*), and *Prosciurillus abstrusus*

Variable	*Sciurus murinus* RMNH 13213[a]	*Sciurus murinus necopinus* USNM 218712[b]	*Sciurus evidens* USNM 217814[b]	*Prosciurillus abstrusus* AMNH 101378[c]
Type	lectotype	holotype	holotype	holotype
Age	adult	very young adult	adult	adult
Sex	female	male	female	female
LHB	—	105	125	134
LT	—	107	107	95
LHF	—	29[33]	33[35]	33[36]
LE	—	—	—	13
ONL	33.1	32.9	36.4	38.2
CBL	29.0	28.7	31.7	34.2
ZB	—	19.4	22.0	23.4
IB	12.2	11.8	13.7	12.4
LN	9.2	9.5	11.0	10.7
LR	15.9	15.1	18.0	17.3
BR	—	5.9	6.9	7.4
MB	15.0	14.6	16.0	16.9
HBC	—	12.8	13.0	14.3
LO	7.9	7.6	7.9	8.3
LD	7.4	6.3	7.0	7.5
LBP	9.3	8.5	9.5	11.6
PPL	—	11.9	13.4	14.4
BBP	6.9	8.5	7.4	8.5
LB	6.5	5.6	6.2	7.0
CLPMM	4.8	5.2	5.6	6.3

[a]Chris Smeenk, at RMNH, measured the skull and dentition.

[b]H.C. Raven obtained values for total length, length of tail, and length of hind feet in the field. He did not measure ear lengths or obtain weights. Musser remeasured the dry hind foot of each skin (values in brackets).

[c]Values for lengths of head and body, tail, hind foot, and ear are those obtained by G. Heinrich, the collector. The value in brackets is Musser's remeasurement of the dry hind foot.

mount; the osteological specimen "*c*" (Jentink, 1887: 190), RMNH 13219, is a skull only. See the account of *P. leucomus* for a description of Forsten's travels through northeastern Sulawesi.

The type locality is "Nord de Célèbes," as listed in Jentink's (1887: 190, 1888: 22) catalogs. Forsten obtained most of his material in the region near the tip of the northeastern peninsula, which is in the administrative district of "Minahasa" (Kabupaten Minahasa), between 1° and 2° N. Sody (1949: 77) restricted the type locality to "the extreme N.E. part of the island," which effectively places the type locality in Kabupaten Minahasa, Propinsi Sulawesi Utara, Indonesia. However, the type locality should rather be defined as "NE Celebes" because Forsten also worked in the environs of Gorontalo and as far west as Paguat (September–November, 1841; see Van Steenis-Kruseman [1950: 179] and Forsten's unpublished diary in the archives of the Leiden Museum); hence, we cannot exclude that one of the specimens is from that region (C. Smeenk, in litt., 2008).

EMENDED DIAGNOSIS: The smallest-bodied of the species of tree squirrels endemic to Sulawesi (see table 3), and further characterized by: **(1)** uniform dark brown upperparts flecked with buff, ochraceous, and black; **(2)** lack of ear tufts, nape patches, middorsal black stripe, or any other patterning formed by different colored stripes and patches; **(3)** dark grayish buff to ochraceous gray underparts; **(4)** tail that is shorter than length of head and body; and **(5)** small, gracile skull (figs. 12–14).

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: Except for the east-central peninsular region, collection localities for *Prosciurillus murinus* are scattered throughout mainland Sulawesi and are also from Talise and Lembeh islands off the coast of the northeastern peninsula (see gazetteer and map in fig. 30). Likely the species can be encountered anywhere on Sulawesi where forest persists, even the east-central peninsula, which has been poorly surveyed for small mammals, especially squirrels.

Prosciurillus murinus is found in forest formations ranging from tropical lowland evergreen rain forest throughout the coasts and middle altitudes to tropical upper montane rain forests in high mountains. On the northern peninsula, voucher specimens come from the coastal plain near sea level to 1700 m on Gunung Klabat and Gunung Ile-Ile, although most examples were collected at places that are scattered between the coastal plain and 1000 m. Kuala Navusu at 30 m and Gunung Latimojong at 2200 bracket the range of elevations at which samples of *P. murinus* have been obtained in the central core of Sulawesi. On the southwestern peninsula, specimens come from 1100 m (Lombasang) and 2000 m (Gunung Lompobatang). Before most of the peninsula was converted from forests to agriculture (see account of *Prosciurillus* sp.), *P. murinus* likely occurred in forests below 1100 m, down to and along the coastal plain.

Only two places on the southeastern peninsula have yielded voucher specimens: Wawo at 50 m near the coast and Masembo at 500 m inland, and this region forms an exception to the altitudinal range of *P. murinus*, extending from coastal plain to mountains, documented in the central core of the island and on the northern peninsula. Montane forests on Pegunungan Mekongga, the mountain range looming above Wawo and Masembo, support populations of *P. abstrusus*, a close relative of *P. murinus*; samples of the former are from 1500 and 2000 m. The lower altitudinal limit of *P. abstrusus* in this highland region and the upper limit of *P. murinus* are unknown.

Pulau Talisei, 8 km northeast of the northwestern tip of the Sulawesi mainland, and Pulau Lembeh, directly off the western coast of the northeastern mainland tip (see map in fig. 28), are the collection sites of the only two insular samples of *Prosciurillus murinus*. Another squirrel, *P. leucomus*, and several other native Sulawesi mammals are recorded from Pulau Lembeh (see the account of *P. leucomus*), but samples of only *P. murinus* and the macaque, *Macaca nigra*, come from Pulau Talisei. That island is separated from the mainland by two smaller islands and water depths of less than 50 m, mostly only 10 m (Sheet NA 51-12). As with Pulau Lembeh, Talisei was most likely part of mainland Sulawesi during Pleistocene glacial intervals when sea level was depressed by at least 120 m, and separated during warm inter-glacial periods (see the account of *P. leucomus*). Neither squirrel nor macaque exhibits any significant morphological contrasts with mainland samples, suggesting relatively recent isolation on Pulau Talisei.

DESCRIPTION: Müller and Schlegel (1844: 87) described *murinus* with this sentence (translated from the original Dutch by Chris Smeenk, in litt., 2008; see appendix 2 for a rendition of the text in Dutch):

> 11.) **Sciurus murinus**, Forsten, n. sp. Appearance and shape as in the preceding species [*Sciurus modestus*, currently a synonym of *Sundasciurus tenuis*, native to peninsular Thailand, Malaya, Sumatra, Borneo, and some smaller islands on the Sunda Shelf; see Corbet and Hill, 1992: 296], but slightly smaller; the tail slightly shorter; the ears less hairy, and the colour more uniform; above mouse-grey and the hairs with whitish yellow tips; below ash-gray. Celebes.

Prosciurillus murinus is the smallest in body size of the species of tree squirrels endemic to Sulawesi (length of head and body, 102–150 mm; length of hind foot, 32–38 mm; weight, 42–110 g; extremes from table 36), and one of the smallest of the tree squirrels and ground squirrels that are native to the Indomalayan region. A few species of Sundaic *Callosciurus* (*C. adamsi* and *C. orestes*) and *Sundasciurus* (*S. lowii*, *S. tenis*, *S. jentinki*, and *S. brookei*) are similar to *P. murinus* in body size; only the species of pygmy tree squirrels in *Nannosciurus* and *Exilisciurus* are smaller (Medway, 1969; Heaney, 1985; Payne et al., 1985).

TABLE 36

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g), Derived from Samples of *Prosciurillus murinus* and *Prosciurillus abtrusus*[a]

Mean ± 1 SD, observed range (in parentheses), and size of sample are listed. Mean values were used to compute LT/LHB. Specimens measured are listed in footnotes.[b]

Variable	*P. murinus* northern peninsula (Pulau Lembeh)	*P. murinus* northern peninsula (Teteamoet, Gunung Klabat, Temboan, Sungai Paleleh)	*P. murinus* central core (Sungai Oha Kecil, Sungai Miu, Sungai Sadaunta, Tomado, Gunung Kanino, Gunung Nokilalaki)	*P. murinus* central core (Kuala Navusu, Sungai Tolewonu)	*P. murinus* southeastern peninsula (Wawo, Masembo)	*P. abtrusus* Pegunungan Mekongga (Tanko Salokko)
HB	126.8 ± 4.71 (123–135) 5	123.5 ± 4.54 (118–130) 8	133.5 ± 9.06 (102–150) 51	137.9 ± 7.23 (126–150) 22	118.5 ± 3.73 (115–125) 6	133.1 ± 8.43 (115–148) 27
LT	108.4 ± 9.86 (93–120) 5	106.3 ± 11.50 (80–115) 8	91.1 ± 14.88 (55–113) 47	96.7 ± 13.72 (65–115) 18	90.3 ± 17.51 (60–108) 6	107.2 ± 14.79 (72–130) 26
LT/LHB (%)	86	86	68	70	76	81
LHF	34.6 ± 1.14 (33–36) 5	33.0 ± 0.54 (32–34) 8	34.6 ± 1.01 (32–36) 51	35.8 ± 1.18 (34–38) 22	33.5 ± 1.05 (32–35) 6	36.0 ± 0.81 (35–38) 30
LE	—	—	13.8 ± 1.04 (10–15) 50	13.5 ± 0.74 (12–15) 22	—	—
WT	—	—	79.2 ± 11.49 (42–100) 51	92.7 ± 14.08 (62–110) 22	—	—

[a]Specimens from the northern peninsula were measured by H.C. Raven in the field. He did not measure ear lengths or obtain weights. Musser remeasured the dry hind foot of Raven's material. Specimens constituting the two samples from the central core of the island were measured and weighed by Musser in the field (see Methods). Squirrels in the samples of *P. murinus* from the southeastern peninsula and *P. abstrusus* were measured by G. Heinrich in the field. He did not obtain weights. Heinrich did measure ear length, from base to crown, which results in a smaller value than notch-to-crown; we have omitted his values because they are not comparable to Musser's notch-to-crown measurements; also we cannot vouch for the accuracy of Heinrich's values for length of head and body and length of tail. Musser remeasured the dry hind feet of Heinrich's material.

[b]Pulau Lembeh: USNM 217810, 217812, 217813, 217814 (holotype of *evidens*), 217815. Teteamoet: USNM 216793, 216794. Gunung Klabat: USNM 217809. Temboan: USNM 217817–19. Sungai Paleleh: USNM 200276, 200278. Sungai Oha Kecil: AMNH 224589–93, 224595. Sungai Miu: AMNH 224046–049. Sungai Sadaunta: AMNH 224043–045, 224596–98, 224601–617, 226836, 226837. Tomado: AMNH 223475, 224050, 224051. Gunung Kanino: AMNH 223536–39, 225492–96, 225499, 225500. Gunung Nokilalaki: AMNH 225497, 225498. Kuala Navusu: AMNH 226063–072, 226074, 226075. Sungai Tolewonu: AMNH 226500–509. Wawo: AMNH 101390–93. Masembo: AMNH 101379, 101394. Pegunungan Mekongga: AMNH 101349–101360, 101362–77, 101378 (holotype of *abstrusus*).

Uniformly dark upperparts, unbroken by contrasting ear tufts, nape patches, midventral black strip, or any other contrasting adornment, and grayish underparts characterize the small and dark *P. murinus*. The dense and short (8–10 mm thick in most specimens) fur covering the upperparts from nose to base of the tail, including the ears and all appendages, is dark brown flecked with buff or ochraceous tints and peppered with black, the middorsal region slightly darker than sides of the head and body. The dark hue, conspicuously darker than seen in species of the *P. leucomus* group or *Rubrisciurus rubriventer*, results from the overhairs that are dark gray for most of their lengths, have a subterminal buff or ochraceous band, and are tipped with black. No tufts or postauricular patches distinguish the small ears from the rest of the dorsum. The eyes are circled by buffy rings.

The dense and short (up to 5 mm thick) fur covering the underparts, from chin to base of the tail, ranges from dark gray washed with pale buff to dark ochraceous gray in most samples (hairs are dark gray for most of their length and tipped with buff or ochraceous tints); a few specimens have dark grayish white venters (tips of the hairs are unpigmented). Most specimens fall in the range between dark grayish buff and ochraceous gray. The demarcation between upperparts and underparts in the latter is not sharp; for example, USNM 219508 from Rano Rano has a solid dark ochraceous gray venter that inconspicuously merges with coloration of the dorsal coat.

The tail is shorter than the length of the head and body (LT/LHB = 68%–86%, see table 36) with the same color pattern as the dorsal fur—long black hairs with alternating distal ochraceous and black bands. Hairs forming tip of the tail are all black.

Females exhibit three pairs of teats, just as in members of the *P. leucomus* complex: one postaxillary pair and two inguinal pairs. A single embryo was found in each of the few females examined.

Views of the small, gracile skull are illustrated in figures 12–14; summary statistics for cranial and dental measurements are listed in tables 37 and 38. Conformations of the skull and teeth are basically miniatures of those elements in the *P. leucomus* group.

COMPARISONS: *Prosciurillus murinus* is markedly smaller in body size than any other species of tree squirrel or ground squirrel endemic to Sulawesi except for the small-bodied *P. abstrusus*, which resembles *P. murinus* not only in body size but coat color. It is between these two that comparisons are required, which we document here.

Prosciurillus abstrusus is still known only by the original 30 specimens collected by Gerd Heinrich in 1932 at 1500 and 2000 m on Pegunungan Mekongga, the highest range on the southeastern peninsula of Sulawesi. In diagnosing the species, Moore (1958: 3) wrote that it "has short white pelage on the backs of the ears which distinguish it from skins of ... *Prosciurillus murinus*; otherwise only size distinguishes the stuffed skins, *P. abstrusus* being larger than *P. murinus*. Moore also noted that *P. abstrusus* had underparts less intensely washed with buff or ochraceous hues.

Mean values of external measurements are greater when the large sample of *P. abstrusus* is contrasted with the very small sample of *P. murinus* from the lowlands of the southwestern peninsula, but such distinctions are not evident between *P. abstrusus* and the larger samples of *P. murinus* from the central core of Sulawesi and the northern peninsula (table 36). The pelage differences described by Moore, however, consistently distinguish the two species. Backs of the ears are covered with fine, short white hairs that form a white mat on all specimens of *P. abstrusus*, but we have not seen this pattern on any example of *P. murinus*—in that species, the fur covering the ears is the same color as the rest of the upperparts. Both *P. abstrusus* and *P. murinus* have similar dark brown dorsal fur in which the buffy or ochraceous hair tips provide a flecking over the dark brown background. The coat averages thicker in *P. abstrusus* compared with lowland samples of *P. murinus* (10–12 mm versus 8–10 mm, respectively), but is comparable in thickness to high mountain samples of *P. murinus*. All examples of *P. abstrusus* have dark grayish white venters (hairs are dark gray basally and unpigmented at their tips); some specimens show a pale buffy wash across the chest, and

a few others have spots or larger patches of pale buff scattered over the venter. Most examples of *P. murinus* have brighter underparts, dark gray washed with buff or richer ochraceous tints; a few match the average in *P. abstrusus*—dark grayish white underparts.

While contrasts between the two species in lengths of head and body, tail, and hind feet are not impressive, *P. abstrusus* has an appreciably larger skull and longer tooth rows than does *P. murinus*. This difference can be appreciated qualitatively by visually comparing skulls of the two species side-by-side (figs. 12–14) and quantitatively by the contrasting mean values for cranial and dental dimensions summarized in tables 37 and 38. Nearly all cranial measurements average greater in the sample of *P. abstrusus* compared with *P. murinus*, and there is no overlap between the samples in the range of values for lengths of bulla and tooth row, and breadth of bony palate. A few dimensions are similar or smaller in *P. abstrusus* compared with *P. murinus*. Typically, the Mekongga squirrel has a relatively narrower interorbit, shorter nasals, rostrum, and diastema relative to occipitonasal length, and an absolutely shorter orbit.

The cranial and dental distinction between the two species is also reflected in the results of multivariate analyses of cranial and dental variables expressed by the distribution of specimen scores projected onto the first and second principal components extracted from principal-components analysis (fig. 31). The projection of scores along the first axis results in two discrete clusters, the one on the left representing all samples of *P. murinus*, that on the right signaling the larger specimens of *P. abstrusus*. Covariation in most dimensions influences this segregation of scores along the first principal component; lengths of bony palate, bulla, and tooth row along with breadths of rostrum and bony palate are especially strong (table 39). *Prosciurillus abstrusus* has relatively shorter nasals, rostrum, diastema, and orbit compared with *P. murinus* as indicated by their large and positive scores along the second axis, and relatively longer tooth rows as reflected by the large negative score for that dimension (table 39).

An osseous qualitative trait can be added to the absolute and proportional cranial dimensional differences between the two species. The smaller-bodied *P. murinus* has a conspicuously higher jugal component of the zygomatic arch, the dorsal border typically forming a high process. The larger-bodied *P. abstrusus* has a lower jugal, its dorsal border smooth or with only a low dorsal process (fig. 14).

Prosciurillus abstrusus inhabits montane forests on Pegunungan Mekongga where it replaces its close relative *P. murinus*. The latter was sampled by G. Heinrich in tropical lowland evergreen rain forest covering the foothills of the Pegunungan at Masembo, 550 m (four specimens), and on the coastal plain at Wawo, 50 m (two individuals). Color and length of the fur of these lowland samples closely resemble those in samples of *P. murinus* from lowlands elsewhere on Sulawesi; the ears of all, for example, are the same color as the neck and back, and the pelage is 8–10 mm thick. We could not quantify cranial differences between the two species because skulls of the six lowland specimens collected by Heinrich are too damaged to obtain complete sets of cranial measurements. The tooth rows, however, remain intact: mean and extreme values for the six (5.1 $\pm$ 0.06, 5.0–5.2 mm) are nested within the range of variation shown by this variable for *P. murinus* (5.2 $\pm$ 0.17, 4.7–5.6 mm, $N = 57$) and not for *P. abstrusus* (6.2 $\pm$ 0.13, 5.9–6.3 mm, $N = 14$).

At present, there is no information revealing how high *P. murinus* extends onto the mountain range or the lowest altitude to which *P. abstrusus* descends. We suspect the altitudinal ranges to be mutually exclusive, their boundaries approximately coinciding with the limits of lower montane forest and lowland evergreen rain forest. This altitudinal exclusion of *P. murinus* from a mountain range and its replacement at those higher altitudes by a different but closely related species is unique to the landscape of the southeastern peninsula. Elsewhere on mainland Sulawesi, populations of *P. murinus* occupy tropical lowland evergreen rain forests on the coastal plain, in middle-altitude hill forests, and up into the mountains where montane forest formations prevail.

TABLE 37
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of *Prosciurillus murinus*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Northeastern peninsula $N = 7$	Pulau Lembeh $N = 4$	Northern peninsula $N = 9$	North-central region 1 $N = 18$	Gunung Lehio $N = 1$
ONL	35.3 ± 0.68 (34.3–36.4)	35.8 ± 1.26 (34.3–37.2)	36.0 ± 0.82 (35.0–37.5)	36.0 ± 0.78 (34.3–37.2)	32.9
CBL	31.1 ± 0.25 (30.7–31.5)	31.3 ± 1.45 (29.5–33.0)	31.8 ± 0.85 (30.4–32.7)	31.7 ± 0.85 (39.5–32.7)	28.7
ZB	21.3 ± 0.70 (20.0–21.9)	21.4 ± 0.97 (20.5–22.4)	22.1 ± 0.81 (21.0–23.3)	21.8 ± 0.53 (20.5–22.5)	19.4
IB	13.1 ± 0.49 (12.3–13.7)	13.0 ± 0.57 (12.3–13.7)	13.1 ± 0.51 (12.0–13.6)	12.9 ± 0.50 (11.8–13.6)	11.8
LN	10.0 ± 0.59 (9.2–10.8)	10.5 ± 0.45 (10.1–11.0)	10.8 ± 0.55 (9.6–11.5)	10.7 ± 0.44 (10.0–11.7)	9.5
LR	16.7 ± 0.37 (16.1–17.1)	17.2 ± 1.09 (15.7–18.0)	17.4 ± 0.45 (16.7–18.0)	17.1 ± 0.53 (16.0–18.0)	15.1
BR	6.0 ± 0.51 (5.2–6.8)	6.5 ± 0.46 (5.9–6.9)	6.0 ± 0.22 (5.7–6.3)	6.2 ± 0.39 (5.5–7.0)	5.9
MB	15.7 ± 0.15 (15.4–15.8)	15.9 ± 0.30 (15.5–16.2)	15.7 ± 0.42 (14.9–16.3)	15.8 ± 0.40 (14.8–16.5)	14.6
HBC	12.8 ± 0.31 (12.4–13.2)	13.0 ± 0.17 (12.8–13.2)	13.0 ± 0.31 (12.5–13.5)	12.9 ± 0.31 (12.1–13.5)	12.8
LO	8.1 ± 0.17 (7.8–8.3)	8.0 ± 0.40 (7.7–8.6)	8.0 ± 0.36 (7.4–8.7)	8.2 ± 0.27 (7.4–8.5)	7.6
LD	7.1 ± 0.23 (6.7–7.4)	7.1 ± 0.48 (6.7–7.8)	7.7 ± 0.35 (7.0–8.0)	7.4 ± 0.34 (6.7–7.8)	6.3
LBP	9.4 ± 0.27 (9.1–9.9)	9.5 ± 0.53 (8.9–10.2)	9.5 ± 0.33 (9.0–10.0)	9.3 ± 0.28 (8.5–9.6)	8.5
PPL	13.0 ± 0.28 (12.5–13.4)	13.2 ± 0.67 (12.3–13.9)	13.1 ± 0.70 (12.0–13.9)	13.3 ± 0.37 (12.5–13.9)	11.9
BBP	7.1 ± 0.23 (6.8–7.4)	17.1 ± 0.21 (6.9–7.4)	7.2 ± 0.26 (6.8–7.6)	7.0 ± 0.20 (6.5–7.3)	6.9
LB	6.4 ± 0.23 (6.0–6.7)	6.2 ± 0.33 (5.7–6.4)	6.3 ± 0.19 (6.0–6.6)	6.4 ± 0.29 (6.1–6.7)	5.6
CLPMM	5.2 ± 0.23 (4.8–5.4)	5.4 ± 0.21 (5.1–5.6)	5.2 ± 0.15 (4.9–5.4)	5.2 ± 0.17 (4.8–5.6)	5.2

GEOGRAPHIC VARIATION: In addition to *murinus*, three other scientific names have been attached to geographic samples of the species, diagnosed primarily by chromatic distinctions of the fur and a cranial measurement, diagnoses inferring the presence of detectable and possibly significant geographic variation within *P. murinus*. Our visual inspection of coat coloration combined with multivariate analyses of data derived from cranial and dental measurements in samples from throughout Sulawesi, however, do not reveal significant geographic variation in these features. Why we disregard the three scientific names (*necopinus*, *evidens*, and *griseus*) as identifying distinctive populations within *P. murinus* is detailed in the section covering synonyms. We explain here why we cannot, using the specimens at hand, identify diagnostic geographic subsets of the species.

In stark contrast to species in the *Prosciurillus leucomus* group, all samples of *P. murinus* closely resemble one another in body size (comparing adults; see table 36) and coloration of the fur covering upperparts and tail—all samples contain a small-bodied, dark squirrel with a tail shorter than the length of head and body. There is a difference

TABLE 38
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of *Prosciurillus murinus*, and from the Sample of *Prosciurillus abstrusus*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	*P. murinus* Rano Rano $N = 2$	*P. murinus* North-central region 2 $N = 16$	Combined samples of *P. murinus* $N = 57$	*P. abstrusus* Pegunungan Mekongga $N = 14$
ONL	34.4 ± 0.57 (34.0–34.8)	37.0 ± 1.06 (35.2–38.6)	36.1 ± 1.16 (32.9–38.6)	38.4 ± 0.73 (37.0–39.3)
CBL	30.7 ± 0.14 (30.6–30.8)	32.6 ± 1.07 (30.9–34.6)	31.7 ± 1.10 (28.7–34.6)	34.2 ± 0.83 (32.8–35.4)
ZB	20.7 ± .71 (20.6–20.7)	22.5 ± 0.69 (21.1–23.4)	21.9 ± 0.86 (19.4–23.4)	23.2 ± 0.83 (22.2–25.0)
IB	12.0 ± 0.07 (11.9–12.0)	13.2 ± 0.44 (12.2–14.0)	13.0 ± 0.54 (11.8–14.0)	13.1 ± 0.59 (12.2–14.4)
LN	10.5 ± 0.57 (10.1–10.9)	11.3 ± 0.65 (10.2–12.5)	10.8 ± 0.68 (9.2–12.5)	10.7 ± 0.54 (9.6–11.6)
LR	16.4 ± 0.71 (16.3–16.4)	17.7 ± 0.65 (16.1–18.6)	17.2 ± 0.72 (15.1–18.6)	17.2 ± 0.44 (16.5–18.0)
BR	5.6 ± 0.07 (5.5–5.6)	6.5 ± 0.44 (5.6–7.2)	6.2 ± 0.44 (5.2–7.2)	7.4 ± 0.43 (6.6–8.3)
MB	15.0 ± 0.07 (14.9–15.0)	16.2 ± 0.44 (15.2–16.8)	15.9 ± 0.48 (14.6–16.8)	16.5 ± 0.37 (15.8–17.1)
HBC	12.6 ± 0.14 (12.5–12.7)	13.2 ± 0.29 (12.8–13.7)	13.0 ± 0.32 (12.1–13.7)	13.9 ± 0.54 (13.0–14.7)
LO	7.8 ± 0.14 (7.7–7.9)	8.4 ± 0.38 (7.6–8.9)	8.2 ± 0.35 (7.4–8.9)	7.9 ± 0.34 (7.1–8.3)
LD	6.9 ± 0.14 (6.8–7.0)	7.6 ± 0.37 (6.8–8.2)	7.4 ± 0.42 (6.3–8.2)	7.6 ± 0.37 (7.2–8.3)
LBP	8.6 ± 0.14 (8.5–8.7)	9.7 ± 0.30 (9.2–10.1)	9.4 ± 0.39 (8.5–10.2)	10.8 ± 0.40 (10.1–11.6)
PPL	12.8 ± 0.00	13.6 ± 0.47 (13.0–14.5)	13.3 ± 0.54 (11.9–14.5)	14.5 ± 0.51 (13.5–15.7)
BBP	6.8 ± 0.14 (6.7–6.9)	17.1 ± 0.18 (6.9–7.5)	7.1 ± 0.22 (6.5–7.6)	8.4 ± 0.24 (8.0–8.7)
LB	6.0 ± 0.00	6.4 ± 0.17 (6.0–6.7)	6.3 ± 0.23 (5.6–6.7)	7.2 ± 0.42 (7.0–8.6)
CLPMM	5.2 ± 0.07 (5.1–5.2)	5.1 ± 0.15 (4.7–5.3)	5.2 ± 0.17 (4.7–5.6)	6.2 ± 0.13 (5.9–6.3)

in thickness of the dorsal coat that is correlated with altitude. The few samples from high mountains, those taken on Gunung Nokilalaki, Pegunungan Latimojong, and Gunung Lompobatang (see gazetteer and map in figure 30), for example, are inseparable in coat color from those collected at lower altitudes, but have a slightly thicker dorsal coat, up to 15 mm in the montane samples; 8–10 mm is the thickness typical of specimens collected in lowlands. But where samples are available from an altitudinal gradient, along Musser's transect from Sungai Oha Kecil at 290 m to Gunung Nokilalaki at 2187 m (see gazetteer and fig. 30), for example, the thicker coat gradually gives way to a shorter coat at the lower collection sites.

There is some geographic variation in coloration of the fur covering underparts of the head and body. Dark gray washed with buff predominates in most samples; others are slightly paler (dark gray tinged with buff) or exhibit a richer hue (dark gray washed with ochraceous). The latter characterizes some samples from the central core of Sulawesi but also a few samples from the northeastern peninsula; paler venters predominate in samples obtained from terrain

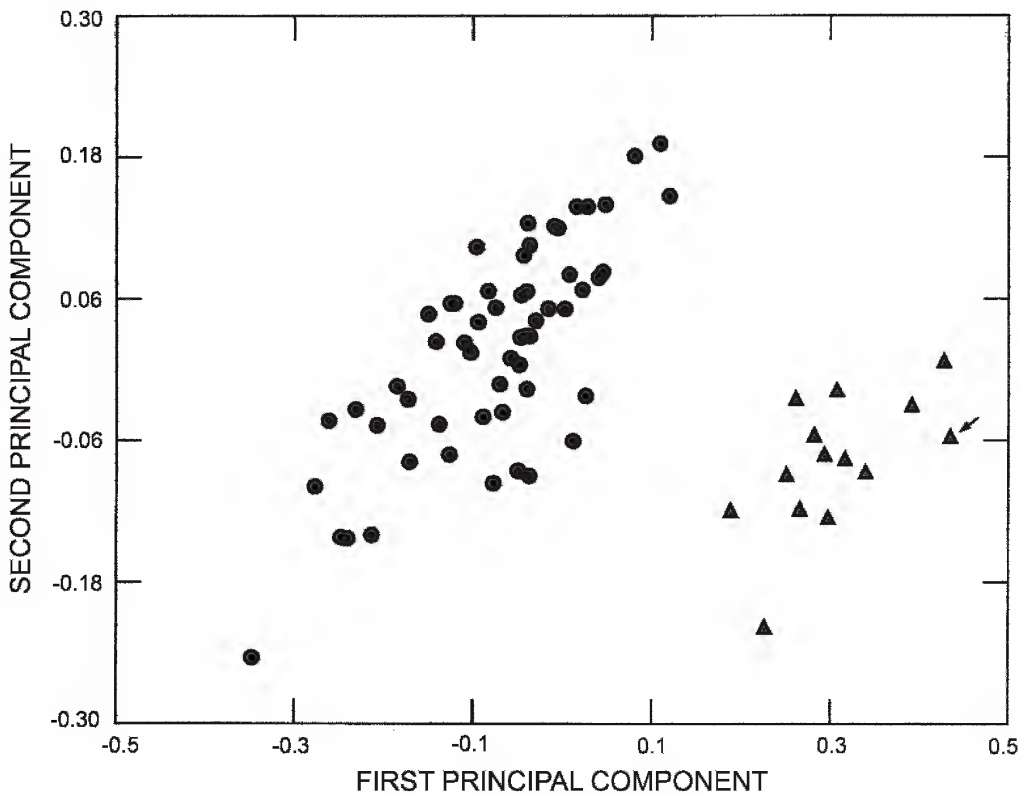

Fig. 31. Specimen scores representing *Prosciurillus murinus* (filled circle; $N = 57$) and *P. abstrusus* (filled triangle; $N = 14$) projected onto the first and second principal components extracted from principal-components analysis. Arrow identifies holotype of *abstrusus*. See table 39 for correlations and percent variance.

between those regions. A gradation from grayish buff to ochraceous gray can even be found within a single population sample. While of potential interest to studies involving coat-color variation, we cannot resolve the chromatic differences we see into geographic patterns that might reflect populations with distinct genetic histories.

Our comparison of data derived from measuring cranial and dental dimensions reveals variation in these quantitative traits that is associated more with age within our adult category than with geographic provenances of the samples. Specimen scores derived from population samples (identified in table 1) and projected onto the first and second principal components extracted from principal-components analysis illustrated in figure 32 form, with an exception, a single constellation without significant substructure pointing to identifiable clusters bounded by particular geographic regions. Scores representing specimens from the northern peninsula, including Pulau Lembeh off the northeastern coast, comingle with those identifying individuals from the central core of Sulawesi. Covariation in most variables spreads the scores along the first principal component (table 40), a measure of size, reflecting both individual variation within an age class, and variation due to age (the range in age from young adults to old adults constitutes the samples). The only striking departure from a single constellation is the score representing the animal from Gunung Lehio, the holotype of *necopinus*, and the only sample collected from that mountain. Its position far to the left in the ordination reflects its smaller skull because the squirrel is younger relative to all the other specimens measured. Although the squirrel is clothed in adult pelage, the cheek teeth are slightly worn and the basisphenoid-

TABLE 39
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus murinus* with the Sample of *Prosciurillus abtrusus*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 31.

Variable	PC1	PC2
ONL	0.035	0.013
CBL	0.039	0.013
ZB	0.036	0.019
IB	0.018	0.021
LN	0.014	0.045
LR	0.018	0.031
BR	0.082	−0.013
MB	0.027	0.013
HBC	0.025	−0.006
LO	0.006	0.031
LD	0.032	0.035
LBP	0.065	−0.002
PPL	0.043	0.009
BBP	0.068	−0.020
LB	0.058	−0.007
CLPMM	0.064	−0.035
Eigenvalues	0.032	0.008
Percent variance	60.251	15.826

presphenoid and basisphenoid-basioccipital sutures incompletely fused.

Three samples we studied are not included in the principal-components analysis. Specimens from Wawo and Masembo in lowlands of the southwestern peninsula (see gazetteer) have badly damaged skulls and we measured only the lengths of maxillary tooth rows. Mean and extreme values for six specimens (5.1 ± 0.06, 5.0–5.2 mm) fall within the range of variation calculated for other geographic samples of *P. murinus* (see tables 37 and 38). We also measured length of the hind foot on the six dry skins (other body measurements recorded by the collector are unreliable and we could not obtain accurate values from the stuffed skins). The mean (33.5 ± 1.05 mm) and extremes (32–35 mm) are also comparable to the range in variation seen in other population samples of *P. murinus* (table 36).

Damaged, juvenile, or missing skulls also excluded samples from Pegunungan Latimojong (2200 m) in the central core of Sulawesi, and Gunung Lompobatang (2000 m) on the southwestern peninsula (Lombasang, 1100 m, Tasoso, 1320 m, and Wawokaraeng, 2000 m; see gazetteer and map in figure 30) from the multivariate analysis using all cranial variables. We did measure lengths of maxillary tooth rows. Two specimens from Pegunungan Latimojong (each with a tooth row of 5.5 mm), and eight specimens from Gunung Lompobatang (5.5 ± 0.15, 5.3–5.7 mm) average slightly greater than in other geographic samples of *P. murinus* (tables 37, 38). We detected no significant difference in coloration of fur between these highland samples and those from comparable altitudes in the central core and northern peninsula of the island, and saw no significant size or conformational distinctions when we compared, side-by-side, the few less damaged skulls with those in other geographic samples. We also obtained mean and extreme values for length of hind foot, which we measured on the dry skins and used as an estimate of body size. (The samples were collected by G. Heinrich and his values for length of head and body along with length of tail are suspect, and we could not remeasure accurately these dimensions on the skins). We measured four specimens from the Latimojong range (34.8 ± 0.50, 34–35 mm) and 10 from the Lompobatang volcano (35.6 ± 0.52, 35–36 mm), which are comparable to the ranges of variation calculated for other population samples of *P. murinus* (table 36).

The pattern of geographic variation in traits associated with coloration of fur and cranial and dental dimensions obtained from samples of *P. murinus* collected from most of Sulawesi is similar to the pattern derived from samples of *Rubrisciurus rubriventer*. Individuals of *P. murinus*, the smallest-bodied of the endemic Sulawesian tree squirrels, and *R. rubriventer*, the largest Sulawesi tree squirrel in body size, are instantly recognizable wherever they are encountered on the island. Unlike species in the *P. leucomus* group where particular color patterns, along with average morphometric distinctions, are tied to different regions of mainland Sulawesi—*P. leucomus* on the northern peninsula, *P. topapuensis* in the highlands forming the western mountain block in the central core of the island, *P. alstoni* occurring over the eastern part of the central core and on the southeastern peninsula, and *P. weberi* at the lower end of the

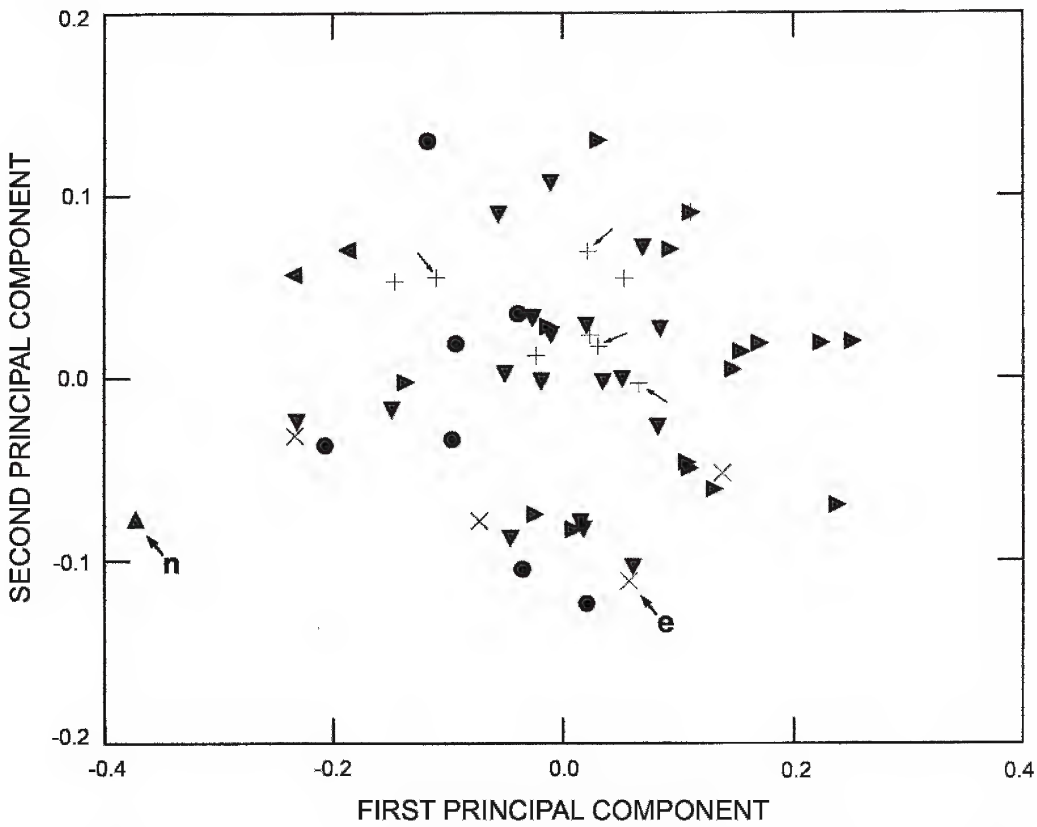

Fig. 32. Specimen scores representing seven population samples of *Prosciurillus murinus* projected onto the first and second principal components extracted from principal-components analysis. Symbols identifying samples are: filled circle = northeastern peninsula (Teteamoet, Gunung Klabat, Temboan; N = 7); × = Pulau Lembeh (N = 4); cross = northern peninsula east of the Minahasa region (Sungai Paleleh, Bumbulan, Ile-Ile; N = 9); filled upright triangle = Gunung Lehio (N = 1); filled inverted triangle = north-central 1 (Sungai Oha Kecil, Sungai Miu, Sungai Sadaunta, Tomado, Kulawi; N = 18); filled left-pointing triangle = Rano Rano (N = 2); filled right-pointing triangle = north-central region 2 (Pinedapa, Kuala Navusu, Sungai Tolewonu; N = 16). Heavy arrows identify holotypes: e, *evidens*; n, *necopinus*. Delicate arrows identify scores representing four AMNH specimens from Bumbulan, which were collected by J. J. Menden between October 10 and 25, 1939. Two others from Menden's sample, collected on October 24, 1939, are in MZB and Sody (1949: 77) had designated one of these as the holotype of "*Sciurillus murinus griseus*" (the holotype is currently stored in RMNH). Musser determined that the two MZB specimens were inseparable in pelage coloration and general external and cranial morphology from the AMNH series, but did not measure them. See table 40 for correlations and percent variance.

central core—no patterns of pelage color and morphometric variation in cranial and dental variables concordant with geographic regions characterize the available samples of *P. murinus* and *R. rubrisciurus*.

ECOLOGY: The diurnal and arboreal *Prosciurillus murinus* is common in understory habitats of primary forest that bracket the range from lowland evergreen rain forest habitats (figs. 8, 22, 23, 33) to montane landscapes (figs. 27, 34, 41, 42), and warm to cool ambient temperatures (table 2); forests along streams, on hillsides, and on ridgetops were all occupied. Musser saw or heard *P. murinus* in the crowns of understory trees, low on the large trunks of high canopy and emergent trees, traveling over trunks and limbs on the forest floor, or foraging on the ground. The squirrels use the limbs and branches of understory trees and their attached woody vines as pathways through the understory canopy. On the ground they

TABLE 40
Results of Principal-Components Analysis Contrasting Population Samples of *Prosciurillus murinus*
Principal components are extracted from a covariance matrix of log-transformed values for 15 cranial and 1 dental variable; see figure 32.

Variable	PC1	PC2
ONL	0.030	0.005
CBL	0.031	0.008
ZB	0.035	0.006
IB	0.031	−0.003
LN	0.044	0.019
LR	0.039	0.006
BR	0.041	−0.056
MB	0.026	0.000
HBC	0.008	0.001
LO	0.031	0.000
LD	0.046	0.013
LBP	0.032	−0.002
PPL	0.030	0.007
BBP	0.016	−0.007
LB	0.021	0.003
CLPMM	−0.000	−0.009
Eigenvalues	0.016	0.004
Percent variance	52.598	13.405

dash along tops of trunks and limbs lying in undergrowth on the forest floor, or dart from beneath one rotting tree trunk or pile of limbs to another. Many squirrels were trapped on tree trunks and limbs lying across streams and ravines (see summary of trapping sites in table 41). Musser saw one squirrel about 40 ft from the ground on the trunk of a canopy tree, but never noticed them any higher. The squirrels may forage into the upper canopy level and crowns of emergent trees, but they move very quickly, and would be difficult to locate unless moving slowly while concentrating on foraging.

In contrast to the wary and quiet *Rubrisciurus rubriventer*, a relative giant inhabiting the same understory habitats as *P. murinus*, the diminutive squirrels are aggressively vocal and not shy. Musser frequently encountered them when checking his traps. Once the squirrels detected his presence they became agitated, scolding from the ground hidden in the undergrowth, from looping woody vines and crowns of small trees, or on the lower trunks of the large canopy formers and emergents. Usually Musser heard the squirrels but could not see them. Those exposed on large tree trunks would soon tire of the confrontation and scurry down the trunk to the ground where they disappeared from sight in the undergrowth. Musser never saw a squirrel run up the trunk into the upper canopy. Vocalizations within the context of these interactions ranged from high-pitched chucks to almost whistles, to bird-like staccatto trills. Durden sometimes saw *P. murinus* in Bogani Nani Wartabone (then Dumoga-Bone) National Park in northern Sulawesi. As he sat quietly on a log removing ectoparasites from anaesthetized forest rats, individual *P. murinus* would occasionally descend to nearby tree trunks and chatter at the human intruder.

Musser occasionally saw *P. murinus* foraging on the ground but mostly in crowns of understory trees or on surfaces of large trunks. Two instances are illustrative. About 30 minutes before dark in lower montane rain forest on Gunung Kanino at 1500 m, Musser watched a squirrel working about 40 ft from the ground in the canopy of a small tree. The squirrel was moving head-first down a tree limb, its body pressed against the bark. It climbed over the lower branches and trunk in slow, jerky movements with its muzzle against the bark and appeared to be scoring the bark or digging into it. The squirrel would cover 2 ft of bark this way, then scamper to another part of the tree and work another section. Musser could not determine whether the squirrel was after a substance in the bark or listening for the movement of insect larvae beneath it.

Another time at about 4:00 P.M., Musser watched three squirrels foraging in the crowns of understory figs that canopied a section of the Sadaunta stream in lowland evergreen rain forest at 800 m. Each squirrel crawled along a branch with its body appressed against the bark, head down. The tail would alternately be held flat out, then quickly twitched upward towards the head, the motion accompanied by a bird-like, loud chirp. As the squirrels crawled along the branch, they occasionally stopped and dug their incisors into the bark, then moved on. They worked along a large branch to where it divided into smaller limbs, then jumped to

Fig. 33. Habitat of *Prosciurillus murinus* in tropical lowland evergreen rain forest at Kuala Navusu, 100 m. The large-bodied *Rubrisciurus rubriventer* and smaller-bodied *Prosciurillus alstoni* were encountered in the same forest. This habitat is similar to that south of Kuala Navusu along the Sungai Tolewonu where the same two species, along with the ground squirrel *Hyosciurus ileile*, were caught. Photographed in 1975.

Fig. 34. Habitat of *Prosciurillus murinus* in upper montane rain forest on Gunung Nokilalaki, 2200 m. The tree squirrel, *Prosciurillus topapuensis*, and ground squirrel, *Hyosciurus heinrichi*, also live here. See table 2 for range of ambient temperatures recorded during the sampling period. Photographed in 1975.

other branches and began again to crawl and gnaw. The three worked over the branches for about 30 minutes, continually flagging their tails and chirping as they went, and occasionally emitting series of deeper chucks and chirps similar to the alarm call. None showed any aggression toward the other; often two would approach one another on the same branch, one working along the top of the limb, the other crawling on the limb's undersurface, passing by and continuing on.

Stomach contents reveal a diet of soft fruits, seeds, and insects (tables 41, 57). Some stomachs contained unidentifiable brown or tan fruit mash from soft fruits; others had remains of figs (the tissuelike endosperm, rubbery rind, and tiny seeds) and large, hard pyramidal seeds from another kind of fruit. Insects recovered from stomachs consisted of macrolepidopteran larvae (caterpillars); geometrid larvae (inch-worm moths); a primitive group of scale insects (Coccoidea, Sternorrhyncha, Margarodidae); arboreal termites (workers and soldiers in Termitidae); small adult beetles (represented by elytras, sclerite fragments, wings, legs, and antennal segments); large adult beetles chopped into pieces; larvae of buprestid beetles (small to large instars); and other kinds of beetle larvae, cockroaches, and cranefly larvae (Tipulidae). Both groups of caterpillars feed on foliage. All the scale insects found are sessile females. Appressed to the surface of bark and leaf stems, they feed by embedding their mouthparts into the vascular system of the tree. Nests of termites are attached to limbs and smaller branches. The buprestid larvae reside beneath bark, other kinds of beetle larvae could be in decaying sections of limbs or beneath bark, and adult beetles roam over surfaces of leaves and bark. The dipteran tipulid larvae live in damp soil, very decayed leaf litter, or very rotting wood on the ground (D. Grimaldi, personal commun., 2009). Cockroaches occur at all levels in the forest.

Some stomachs contained mostly fruit with only a few insects; others were packed with remains of caterpillars, scale insects, or termites along with a bit of fruit. The small caterpillars and beetle larvae were ingested whole, the larger species were usually chewed into pieces; scale insects were either intact or had been rendered into chewed fragments. Adult beetles were always represented by chewed fragments in the stomachs. The squirrels glean the caterpillars from the leaves, pick off the scale insects from surfaces of branches, scratch the termite nests and grab the insects as they pour out, dig into bark for the beetle larvae, and snatch adult beetles and cockroaches from leaves and tree limbs. On the ground they would scratch out the tipulid larvae, and also pick off any adult beetles or cockroaches encountered.

Musser caught only one squirrel in a live-trap. It ignored all foods offered and was released the next day.

ECTOPARASITES: A sucking louse *Hoplopleura murinus*, n. sp. (see following section for description), uniquely parasitizes *Prosciurillus murinus* (table 56). This small-bodied squirrel is also the host for two species of flea (Siphonaptera, Pygiopsyllidae): *Farhangia quatturordecimdentata* is recorded from voucher hosts collected at Tomado and Sungai Oha Kecil in central Sulawesi (Mardon and Durden, 2003), and *F. celebensis* was found on hosts obtained from Pulau Lembeh off the northeastern coast of the northern peninsula (Ewing, 1924; Traub, 1980). *Farhangia quatturordecimdentata* is also parasitic on the arboreal murid rodent, *Margaretamys beccarii*, another Sulawesian endemic confined to lowland tropical evergreen rain forest (Musser, 1982), but *Farhangia celebensis* is known only from *Prosciurillus murinus* (Mardon and Durden, 2003). *Farhangia* spp. are "nest fleas" (Traub, 1980) and would therefore be expected to be more common in nests of *P. murinus* than on the host. Ectoparasitic laelapid mites were recovered from *P. murinus* pelt AMNH 224589 collected at Sungai Oha Kecil in central Sulawesi in 1974 at an elevation of 290 m.

SYMPATRY: Over mainland Sulawesi, the geographic range of *P. murinus* overlaps those of *Rubrisciurus rubriventer*, both species of *Hyosciurus*, and all species of *Prosciurillus* except for *P. abstrusus* (table 6). *Prosciurillus murinus* and *P. leucomus* are also sympatric on Pulau Lembeh, off the coast of the northeastern peninsula (table 5). Along his transect in the northern portion of central Sulawesi, Musser trapped *P. murinus* in the same traplines, and sometimes in the same

TABLE 41

Summary of Habitat at Trapping Sites, Stomach Contents, and Other Relevant Information for Specimens of *Prosciurillus murinus* Collected by Musser in Central Sulawesi, 1973–1976

Collection locality, specimen number, elevation, and month and year of collection are included. Descriptions of the trapping sites and contents of stomachs, slightly edited, are from Musser's field journals (in mammalogy archives at AMNH). Six of the collection localities (Sungai Oha Kecil, Sungai Miu, Sungai Sadaunta, Tomado, Kuala Navusu, and Sungai Tolewonu) are in tropical lowland evergreen rain forest; lower montane rain forest describes the places on Gunung Kanino, and Gunung Nokilalaki is mantled in tropical upper montane rain forest. With exceptions as indicated, all squirrels were caught during the day in Conibear traps (rats taken in the same traps were caught during the night). Unless noted differently, trapping sites were in primary forest formations.

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
Sungai Oha Kecil			On small, dry but rotting trunk lying across stream.
224589 (1757)		Aug. 1974	
224590 (1867)	290		
224591 (1709)	290	Aug. 1974	In runway beneath rotting trunk lying on ground in partially cut forest covering stream terrace.
224593 (1877)	427	Aug. 1974	On living trunk sprouting leafy branches lying across stream in good forest.
224592 (1886)	396	Aug. 1974	On trunk, still sprouting shoots, lying over stream suspended between rocks about 10–12 ft above water surface.
224594 (1898)	488	Aug. 1974	On rotten *Pandanus* trunk (smooth, damp, no moss, vines, or other vegetation covering it) lying across stream 3 ft above water level. Streamside slopes steep but well covered with good undergrowth and forest of short trees, palms (including *Pigafetta*) and *Pandanus*. The rat, *Paruromys dominator*, was trapped at same spot.
224595 (1887)	488	Aug. 1974	On sprouting and vine-covered trunk lying across stream in good streamside forest.
Sungai Miu		Mar. 1974	On tree growing over stream in streamside forest.
224046 (1483)	350		
224047 (1484)	350	Mar. 1974	On top of pile of dead limbs at the bottom of a steep bank next to river. **Stomach**: empty except for remnants of reddish brown fruit.
224048 (1511)	350	Mar. 1974	On wet, decaying trunk straddling stream, caught in early morning. **Stomach:** nearly empty, some old fruit mash and a sprinkling of termite (Termitidae) remains.
224049 (1536)	350	Mar. 1974	On wet, decaying trunk lying across stream in thick streamside forest. **Stomach:** nearly empty, masticated pieces of one or two small adult beetles; no fruit.
Sungai Sadaunta 224043 (1434)	675	Feb. 1974	Five ft above ground on top of huge rotting trunk of giant canopy tree lying in dense understory (shrubs, ferns, crisscrossed by woody vines) in primary forest adjacent to stream. A *Rubrisciurus rubriventer* and the rat, *Taeromys celebensis*, were caught in same spot. **Stomach**: full of reddish brown soft fruit remains, some pieces of fig, numerous macrolepidopteran caterpillar larvae and a few termitid termite soldiers.
224044 (1435)	675	Feb. 1974	On rotting trunk lying across stream in primary streamside forest. Stomach empty.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
224045 (1439)	675	Feb. 1974	On rotting, dead limb, covered with leafy vines, lying across stream in primary streamside forest. The rats, *Rattus hoffmanni* and *Maxomys musschenbroekii* were trapped on same spot. **Stomach:** partially full of same reddish brown fruit mash as found in other *P. murinus* stomachs along with remains of a macrolepidoptern caterpillar and legs from small adult insects, probably beetles.
224601 (2089)	762	Oct. 1974	On rotting, smooth and wet trunk lying across a steep ravine in hillside forest below trail and above camp. The rat, *Maxomys musschenbroekii* was caught at same spot.
224602 (2092)	762	Oct.1974	On wet, smooth and rotting trunk lying across stream near camp in streamside forest. A *Prosciurillus topapuensis* and a rat, *Maxomys musschenbroekii*, were taken in same spot.
224603 (2124)	762	Oct. 1974	On trunk lying across stream near camp, caught about 10:00 a.m. **Stomach**: fullof fig remains (mostly the rubbery rind with some tiny black seeds still attached to the inner tissue), a few hard and black pyramidal seeds enclosed in tissue, and pieces of at least one small adult beetle (sclerites, elytra, wings, legs, antennae).
224604 (2399)	777	Dec. 1974	On rotting, moss-covered trunk, partially covered by vines and ferns, lying across Sungai Sadaunta upstream from camp. A *Rubrisciurus rubriventer* and the rat, *Maxomys musschenbroeki*, were trapped in same spot.
224596 (2062)	823	Sept. 1974	On wet, decomposing wanga (*Pigafetta filaris*) palm trunk lying across Sungai Sadaunta about 200 ft upstream from where *Rubrisciurus* ASE 2033 was trapped (see table 10). A *Prosciurillus topapuensis* was trapped at same spot on a different day.
224597 (2303)	823	Nov. 1974	On rotting, wet trunk (free of vegetation) lying across stream in dense understory of streamside forest. Just downstream the rat, *Crunomys celebensis*, was trapped on the stream terrace.
224605 (2060)	823	Sept. 1974	On huge, rotting, moss-covered trunk lying across Sungai Sadaunta in good streamside forest. Several examples of the rat, *Paruromys dominator*, were trapped nearby.
224606 (2072)	823	Sept. 1974	On wet, rotting wanga palm trunk lying on top of rocky terrace next to and above Sungai Sadaunta. Just downstream is a long trunk on which *Rubrisciurus rubriventer* ASE 2033 was caught (see table 10).
224607 (2154)	823	Oct. 1974	On wet, rotting wanga palm trunk straddling deep ravine running into Sungai Sadaunta. The rats, *Bunomys chrysocomus* and *Rattus marmosurus* were trapped at same spot; several *B. chrysocomus* were trapped on an adjacent terrace.
224598 (2224)	854	Oct. 1974	On decaying, wet trunk lying through thick undergrowth of ferns, shrubs, and gingers over small stream just above trail in steep hillside forest. **Stomach**: full of tan fruit mash with chewed and cut pieces of a few macrolepidopteran caterpillars.
224608 (2079)	854	Sept. 1974	On long, wet, and decaying wanga palm trunk lying 5 ft above and across Sungai Sadaunta just upstream from area where some rats, *Paruromys dominator*, were trapped. The rat, *Rattus hoffmanni* was trapped in same spot as ASE 2079.
224609 (2170)	854	Oct. 1974	On wet and decaying wanga palm trunk lying across stream; trunk is smooth and free of vegetation.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
224610 (2171)	869	Oct. 1974	On rotting, half-shredded wanga palm trunk lying across Sungai Sadaunta only a few feet upstream from where a rat, *Paruromys dominator*, was caught on a different trunk bridging the stream. *Prosciurillus topapuensis* was caught at same spot on a different day.
224599 (2265)	884	Oct. 1974	On same moss-covered rotting limb and trunk lying on terrace adjacent to stream where two of the rats, *Paruromys dominator*, were also trapped, just upstream from where the rat, *Echiothrix centrosa*, was taken.
224611 (2125)	884	Oct. 1974	On moss and fern and epiphyte-covered large root from a huge canopy fig growing on edge of the stream terrace; root projects from base of tree across stream to other terrace, 7–10 ft above the water; the straddling root is nearly concealed by a covering mantle of moss, ferns, and epiphytes.
224600 (2266) 224612 (2311)	915	Oct. 1974	On limb of understory tree growing from one bank to the other over the main upper tributary of the Sungai Sadaunta. The trunk springs from one margin of the stream, leaning over it with its upper branches reclining on the opposite terrace. The main connecting limb (3–5 in. diameter) is covered by moss that is trampled down, indicating frequent use by small mammals. Trap was set about 7 ft above stream level. No. ASE 2311 was caught during November. The arboreal rat, *Rattus marmosurus*, was trapped in same spot.
224613 (2316)	915	Nov. 1974	On thick, smooth, dead limbs lying across upper tributary of Sungai Sadaunta. Limb is free of vegetation or moss, extends from one eroded bank up and over 2 ft above the water and down to the other bank; each bank is at stream level in a wide ravine below high narrow terraces. The rats, *Bunomys* sp. and *Maxomys* sp., were trapped on same spot.
226836 (4341)	930	Mar. 1976	On limb of understory tree growing across ravine containing main upper tributary of the Sungai Sadaunta; base of the trunk is at edge of stream, with the trunk leaning over the water and its upper branches reclining on the opposite terrace. The main connecting limb (3–5 ft in diameter) on which the trap was placed is mossy, and the moss is trampled, indicating frequent use; trap set about 7 ft from stream level. In 1974, examples of three kinds of squirrels (the ground squirrel, *Hyosciurus ileile*; the tree squirrels, *Prosciurillus topapuensis* and *Rubrisciurus rubriventer*) and an arboreal rat (*Rattus marmosurus*) were taken in the same spot.
224614 (2361)	976	Nov. 1974	On rotting large trunk covered with moss, shrubs, and ferns lying across headwater tributary of Sungai Sadaunta—steep sides of stream ravine supports dense wanga palms; figs form a dominant component of the understory.
226837 (4347)	976	Mar. 1976	Caught during morning before 7:00 a.m. on top of huge rotting trunk (4 ft diameter) that extends from one high terrace across stream to the opposite terrace. **Stomach:** nearly empty, a bit of fruit debris mixed with a few remains of macrolepidopteran caterpillars.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
224615 (2317)	991	Nov. 1974	On wet, moss-covered decaying limb lying across main headwater tributary of Sungai Sadaunta. Canyon here is V-shaped, covered with short forest typical of steep slopes near ridgetops. Understory figs are abundant along stream and form canopy over it; woody vines, the palm *Caryota*, occasional sugar palms, scattered wanga palms, many ferns, shrubs, and rattan comprise the streamside vegetation. The rat, *Bunomys* sp., was trapped at same spot.
224616 (2328c)	1006	Nov. 1974	On decaying trunk lying on stream terrace in thick ferns and rattan upstream about 10 ft from where the rat, *Taeromys celebensis*, was caught.
224617 (2336)	1037	Nov. 1974	On branch lying through understory and extending across a shallow ravine, 3 ft off ground, in low shrubby forest between stream and trail.
Tomado 223021 (524) 223022 (525)	1000	Aug. 1973	Two traps set on two trunks straddling narrow stream in mature forest. Both squirrels were caught during same day.
223475 (552)	1000	Aug. 1973	On trunk lying in mature forest; trunk is part of large tree-fall that opened canopy in forest.
224050 (1621)	1000	May 1974	On decaying, moss-covered trunk bridging narrow steam in primary forest. **Stomach**: full of reddish brown soft fruit mash, packed with whole and chewed scale insects (Coccoidea, Sternorrhyncha, Margarodidae), and a few small geometrid caterpillars (larvae of inch-worm moths) representing two species.
224051 (1622)	1000	May 1974	On decaying, moss-covered trunk lying across narrow steam in primary forest, just upstream from where ASE1621 was caught. **Stomach**: full of reddish brown remains of fig; pieces of macrolepidopteran caterpillars.
Gunung Kanino 225492 (2535)	1402	Feb. 1975	On small living branch of understory tree growing low across Sungai Salubeka. **Stomach**: partially filled with tan and gray fruit mash.
225493 (2446) 225496 (2449)	1418	Jan. 1975	On decaying, wet jumble of trunks and limbs from an old tree-fall straddling narrow stream below camp. A *Rubrisciurus rubriventer* was trapped on same spot on a different day. **Stomach of ASE 2449**: full of tan fruit mash.
225494 (2478)	1418	Feb. 1975	On wet, clear and rotting trunk lying across Sungai Salubeka near camp.
225499 (2517)	1418	Feb. 1975	On rotting trunk, wet and clear of moss and other vegetation, lying across small stream at bottom of shallow ravine with very wet and muddy slopes.
225492 (2535)	1402	Feb. 1975	On small living branch of understory tree growing low across Sungai Salubeka. **Stomach:** partially full of tan and gray fruit; no insects.
223536 (849)	1463	Nov. 1973	On trunk 2 ft from forest floor; caught about 8:00 a.m.
223538 (924) 223539 (935)	1463	Nov. 1973	On dry but decaying trunk 2 ft from ground, lying over slope near hillside next to river. The rat, *Bunomys penitus*, was trapped at same spot.
225500 (3046)	1494	May 1975	On decaying trunk (6 in. diameter, top clear, sides mossy) lying across stream extending from terrace to the opposite terrace and 5 ft above water surface. A *Prosciurillus topapuensis* was trapped at same spot on a different day.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
223537 (875)	1585	Nov. 1973	In runway beneath large rotting, moss-covered trunk in rattan understory of dammar (*Agathis*) grove.
Gunung Nokilalaki 225497 (2856)	2134	Apr. 1975	On ground in front of earth and rock face just above supply stop on trail.
225498 (2587)	2187	Mar. 1975	Sherman live-trap on ground in damp runway alongside rotting, moss-covered trunk lying on wet, rocky slope in moss forest. Caught about 10:00 a.m.
Kuala Navusu 226063 (3091)	31	Sept. 1975	On trunk (diameter 5 in.) of tree that had fallen across stream, connecting the stream terrace on one side to the opposite bank and bordering forest, trunk 5 ft above surface of water, just up from camp; caught yesterday in evening. Four *Prosciurillus alstoni* were trapped at same spot during different days.
226064 (3123)	31	Sept. 1975	On live trunk (6 in. diameter) growing across dry ravine on steep hillside below camp. Good hillside forest, broken in a few places by rotting tree-falls. **Stomach**: full of mostly brown fruit mash, many tiny larvae (small versions of those in ASE 4174), a few termitid termite workers (heads), several small macrolepidopteran caterpillars.
226065 (3155)	31	Sept. 1975	On a decomposing *Livstonia* palm trunk lying across stream near end of trapline. High, dense scrub covers streambanks in hillside forest partially thinned of canopy trees. *Rubrisciurus rubriventer* and rat, *Maxomys hellwaldii* were trapped at same spot. **Stomach**: full of reddish brown fruit mash mixed with remains of numerous small macrolepidopteran caterpillars.
226066 (3384)	31	Oct. 1975	On long, smooth trunk of *Livistona* palm that had fallen across part of stream terrace, connecting one terrace with that on the other side of the stream; trunk about 10 ft above water surface. A *Prosciurillus alstoni* was caught in same spot on a different day.**Stomach:** nearly empty, two geometrid caterpillars (larvae of inch-worm moths), tiny bits of debris.
226067 (3317)	38	Sept. 1975	On rotting trunk (10 in. diameter) bridging tributary stream. Caught during late morning drizzle. **Stomach:** full of mostly fruit mash and remains of a few scale insects (Coccoidea, Sternorrhyncha).
226068 (3347)	38	Oct. 1975	On decaying section of tree limb (10–12 in. diameter) lying across creek; caught in morning between 7 and 10:00. **Stomach**: full of semi-dry compact mass of purple and pale yellow fruit mash with pieces of skin.
225909 (3354)	61	Oct. 1975	On decaying branch straddling wet ravine. The branch is part of a rotting, tall canopy tree that fell and bridged the ravine connecting a ridge with the opposite hillside. Forest is open on either side of the huge trunk, limbs, and branches, and only scrub has regrown. Gingers and elephant ears cover slopes near the trunk, young *Macaranga* and hereau (*Pinanga*) palms are common along margins of the opening. Tall understory trees form a closed canopy at either side of the tree-fall opening; slopes are steep and muddy, partial leaf cover. The rat, *Maxomys hellwaldiii*, was trapped on the ground beneath the trunk.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226069 (3583)	46	Nov. 1975	On trunk (6 in. diameter) lying across rocky tributary bounded by steep hillsides. Examples of the rat, *Bunomys andrewsi*, were caught nearby. **Stomach**: packed with remains of geometrid caterpillars (larvae of inch-worm moths) mixed with a little fruit mash.
226070 (3178)	55	Sept. 1975	On long, decaying trunk lying on ground down side of slope above tributary stream. The trunk is part of a tall, huge canopy tree that fell down the hillside from upslope. The bole still lays down the hill providing a path on which rats and squirrels can run downslope above the ground; surrounded by tall hillside forest. Examples of the rat, *Paruromys dominator*, were caught in on an adjacent limb of the same tree. **Stomach:** partially full of unidentifiable carmel-colored soft fruit mash and numerous chewed pieces of scale insects (Coccoidea, Sternorrhyncha, Margarodidae).
226071 (3596)	107	Nov. 1975	On mossy, decaying trunk (1 ft diameter) that lay across the rocky stream bed of main stream where it was becoming steep. Good hillside forest on either side. Squirrel caught about 8:00 a.m., just before we got to trap. **Stomach:** empty.
226072 (3348) 226073 (3368)	139	Oct. 1975	On smooth trunk (8 in. diameter) lying across rocky slope in open understory above Siuri and near base of large, clifflike outcrop. Trunk lay about 3 ft above ground for most of its length, about 60 ft long. Caught ASE 3348 day before in late afternoon, ASE 3368 in early morning a few days later. **Stomach of ASE 3348:** partially full of mostly mash from small figs.
226074 (3407)	182	Oct. 1975	On rotten section of trunk (2 ft diameter) lying horizontally on steep slope and extending across deeply cut rocky streambed to other slope; part of an old tree-fall that spread its trunk sections down the ravine. Good understory canopy. **Stomach:** partially full: gray, claylike substance, unidentifiable.
226075 (3296)	229	Sept. 1975	On rotten trunk (6 in. diameter) lying across damp ravine that is well shaded by rattan and understory trees on steep slope above tributary stream. Caught *Prosciurillus alstoni* at same spot on a different day. The rat, *Maxomys hellwaldii*, was taken on ground nearby.
Sungai Tolewonu 226500 (3915)	152	Jan. 1976	On decaying trunk lying across deep tributary, near another trunk where a rat, *Paruromys dominator*, was caught. **Stomach:** partially full of pink fruit mash and a chunk of pinkish purple buprestid beetle larva (like those in *P. alstoni* ASE 3366).
226501 (3929)	152	Jan. 1976	On trunk of living *Pometia pinnata* (10 in. diameter) that had been uprooted and fallen across ravine; trunk is covered with moss and branches that have sprouted leaves all the way along trunk, and sits about 15 ft above water in bottom of ravine. Short forest on either side; thick understory; very rocky. **Stomach**: full of soft fruit remains.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226502 (4258)	152	Feb. 1976	On rotting trunk of canopy tree (1.5–2 ft diameter, 50 ft long) bridging the main river about midway between first and second large tributaries. Trunk rests 4–7 ft above water level and is covered with thick moss on two sides and supports a few small shrubs, ferns, and palm seedlings scattered along its length—not enough that provides any decent cover. Along middle of trunk is a moss-free runway, about 5 in. wide that extends entire length (apparently a path frequently used by rodents to cross the river). On one side of the river is terrace forest, on the other side is steep, moss-covered rocky slope that gives way above to hill forest. Five *Rubrisciurus rubriventer* and a rat, *Paruromys dominator*, were taken in same spot. **Stomach**: full of tan fruit mash and chopped segments of a large adult beetle (mostly pieces of thorax and abdomen, two legs, no head).
(4174)	166	Feb. 1976	On large rotting *Pometia* trunk (1.5 ft diameter, 45 ft long) bridging main river, extending from flat river terrace on one side to rocky hillside on the other bank, and about 5 ft above water level. Trunk is free of vegetation; a limb from a live tree runs along the side of the trunk and its leafy branches provide partial cover over the top surface of the *Pometia*. The tree squirrels, *Prosciurillus alstoni* and *Rubrisciurus rubriventer*, and the rat, *Maxomys hellwaldii*, were taken on same trunk. **Stomach**: full of brown fruit mash and some worker termitid termites.
226503 (3909) 226504 (3952)	183	Jan. 1976	On large limb (10 in. diameter) of *Pometia* that had fallen from a canopy tree on bank; limb is wet and smooth, no moss. The stream is wide here with a vegetation-covered rocky island in middle; branch rests on rocks, one end in stream, the other ends on sections of old, rotten and moss-covered trunk that lay across from rocks to steep slope. ASE 3952 caught about 6:30 a.m. **Stomach of ASE 3952:** full of brown fruit mash mixed with one small beetle larva. **Stomach of ASE 3909**: full of reddish brown fruit mash, one large macrolepidopteran caterpillar, remains of a few scale insects (Coccoidea).
226505 (4138)	198	Feb. 1976	Caught before 8:00 a.m. on trunk lying across left fork of third long tributary. Trunk (8 in. diameter, 30 ft long) is dry and free of moss, extending from low hillside across the stream to a terrace; trunk rests a foot above water surface. *Prosciurillus murinus* is common in the understory forest bordering the tributary; the squirrels are heard calling but rarely seen. **Stomach**: partially filled with brown fruit mash and numerous remains of termitid termites.
226506 (4070)	213	Jan. 1976	On rotten section of wet, mossless trunk (40 ft long, 8–10 in. diameter) that lay in understory on slope above tributary stream; one end of trunk rests on side of streambed, the other on slope in dense understory. Several pieces of rotten wood are scattered here, part of an old tree-fall; ground is wet and crumbling; good forest; trunk is about 2 ft off ground for most of its length. **Stomach**: full of mostly tan and brown fruit mash, looks like the same kind of stuff found in stomachs of the rats *Maxomys hellwaldii* and *Paruromys dominator*; also remains of a few small beetles.

TABLE 41
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site and other information
226507 (4175)	229	Feb. 1976	On rotten trunk (8 ft long, 20 in. diameter), smooth, free of moss and shrubs, lying across small ravine confluent with left-hand fork of third large tributary; wet streamside forest. **Stomach:** partially full of brown fruit mash and insects (pieces of macrolepidopteran caterpillars, small beetle larva with legs, many dipteran larvae of Tipulidae, and remains of a cockroach).
226508 (4051)	244	Jan. 1976	On dry limb (4–6 in. diameter) lying across ravine about 10 ft above water surface; ravine at its banks are 10 ft across; caught early in morning. **Stomach**: full of mostly tan fruit mash with chewed remains of macrolepidopteran caterpillars and a beetle larva.
226509 (4052)	305	Jan. 1976	On slender trunk (4 in. diameter) lying across steep-sided ravine of branch of main tributary in headwaters area. Trunk bridges ravine about 15 ft above water surface. **Stomach**: a bit of gray substance, otherwise empty.

traps, as the tree squirrels *R. rubriventer*, *P. topapuensis*, *P. alstoni*, and the ground squirrels *H. heinrichi* and *H. ileile* (see table 41).

SYNONYMS: Information covering the three synonyms of *P. murinus*, and reasons behind their allocations are summarized below.

Sciurus murinus necopinus Miller and Hollister, 1921: 98. HOLOTYPE: USNM 218712 (museum study skin and complete skull; measurements are listed in table 35), a very young adult male collected by H.C. Raven (original number 3107) on January 20, 1917. TYPE LOCALITY: Gunung Lehio, 01°33′S, 119°53′E, above 6000 ft (1829 m; locality 42 in gazetteer and map in figure 30), in the western portion of the central core of Sulawesi, Propinsi Sulawesi Tengah, Indonesia.

Based on nine specimens from Gunung Lehio, Kulawi, Pinedapa, and Rano Rano in the central core of Sulawesi, Miller and Hollister (1921: 98) diagnosed *necopinus* as "Like *Sciurus murinus murinus* Müller and Schlegel, from Menado, North Celebes, but skull with decidedly smaller auditory bullae." After presenting measurements, they remarked (p. 99) that "This subspecies reaches its extreme form in the high mountains of the interior of Middle Celebes. Specimens from Pinedapa near the coast of the Gulf of Tomini, near Mapane, show an approach toward the typical race of North Celebes."

For Miller and Hollister, the name *necopinus* identified USNM samples from the central core of Sulawesi. Multivariate analyses of cranial and dental variables, which includes an estimate of bullar size, for the USNM specimens examined by Miller and Hollister and those collected by Musser along his transect from lowlands at the Sungai Oha Kecil to the highlands of Gunung Kanino and Gunung Nokilalaki (see tables 37 and 38), did not separate the central Sulawesian samples from those collected on the northern peninsula, the northeastern tip, or Pulau Lembeh (see map in fig. 30). In the graph of specimen scores projected onto the first and second principal components extracted from principal-components analysis illustrated in figure 32, the only striking departure from a single constellation of scores is the score representing the animal from Gunung Lehio, the holotype of *necopinus*. Its position far to the left in the ordination (table 40) reflects its smaller skull because the squirrel is younger relative to all the other specimens measured. Although clothed in adult pelage, the cheek teeth are slightly worn and the basisphenoid-presphenoid and basisphenoid-basioccipital sutures are open.

Squirrels in some samples from the central core of Sulawesi tend to have darker under-

parts (a rich ochraceous gray) than samples from other geographic regions, but there is geographic overlap in this chromatic feature. The series from Teteamoet in the northeastern limb of the northern peninsula, for example, is inseparable from the richly pigmented specimens collected at Pinedapa in the central core of the island.

We have not uncovered unique chromatic or morphometric traits identifying samples from the central core of Sulawesi as representing a population significantly different from that ranging over the northern peninsula and on Pulau Lembeh.

Sciurus evidens Miller and Hollister, 1921: 99. HOLOTYPE: USNM 217814 (museum study skin and complete skull; see table 35 for measurements), an adult female collected by H.C. Raven (original number 3176) on August 23, 1917. TYPE LOCALITY: Pulau Lembeh, 01°26′N, 125°13′E (elevation of collection site is not recorded but highest point of the island is 447 m; locality 5 in gazetteer and map in figure 30), of the coast of the northeastern end of the northern peninsula of Sulawesi, Propinsi Sulawesi Utara, Indonesia.

"Like *Sciurus murinus* Müller and Schlegel, from the mainland of Celebes, but paler, decidedly more yellowish or rusty brown" is how Miller and Hollister (1921: 99) diagnosed *evidens* based on six specimens from Pulau Lembeh. They remarked that "The paler, more yellowish brown coloration of this form makes the animal conspicuously different from the dark, richly colored *Sciurus murinus* of the neighboring mainland of Celebes."

We examined all of Miller and Hollister's specimens from Pulau Lembeh and the adjacent mainland and failed to see their diagnostic chromatic distinction between island and mainland samples. Covariation in cranial and dental dimensions also do not result in two separate clusters of specimen scores projected onto first and second principal components extracted from principal-components analysis (fig. 32, table 40). Scores representing specimens in the type series of *evidens* are scattered throughout the compact constellation of points for squirrels in our samples from the northern peninsula and central core of Sulawesi. We have no evidence to indicate that the squirrels collected by Raven on Pulau Lembeh represent anything other than an insular population of *Prosciurillus murinus*, an assessment made earlier by Ellerman (1947: 259): "A specimen of *Prosciurillus evidens* Miller and Hollister, from Pulau Lembeh off North Celebes has been received at the Museum, and I consider it to be a synonym of *P. murinus*."

Sciurillus murinus griseus Sody, 1949: 77. HOLOTYPE: RMNH 9827 (formerly MZB 5974; museum study skin, skull missing; skull and mandible were at Leiden in 1951 when G.H.H. Tate photographed them, but both elements cannot now be located in the collection; C. Smeenk, in litt., 2008), an adult female collected by J.J. Menden on October 24, 1939. TYPE LOCALITY: Bumbulan, 00°29′N, 122°04′E, coastal plain near sea level (locality 13 in gazetteer and map in figure 30), on the southern coast of the northern peninsula of Sulawesi, Propinsi Sulawesi Utara, Indonesia.

In addition to the holotype, Sody studied two other females collected by Menden from Bumbulan. Those three are part of a larger sample from Bumbulan obtained by Menden in 1939, ten of them currently stored in AMNH (see gazetteer). Sody (1949: 77) diagnosed *griseus* this way:

> While in freshly collected *murinus* the underside is mousecoloured, suffused with tawny buff, in *griseus* the hairs on the underside, which have also mouse-colored bases, possess rather long grey tips slightly tinged with buff. In general appearance the ventral side is much lighter than in the typical race.
>
> The auditory bullae are a trifle smaller than in typical *murinus*. Strange enough, for *necopinus* Miller & Hollister, the authors do not mention difference in colour from *murinus* of Menado.

In our samples of *P. murinus* from throughout Sulawesi, the underparts range from dark gray speckled with white or pale buff to dark ochraceous gray, with most specimens falling within the range between dark grayish buff and ochraceous gray. The specimens from Bumbulan, including the holotype of *griseus*, fall close to the dark grayish buff end of the spectrum and in this respect are inseparable from some samples

collected at places in the northern, central, and southeastern regions of the island.

We could not measure the skull from the holotype of *griseus*, but did obtain values for cranial and dental dimensions from four intact adult skulls in Menden's sample from Bumbulan housed at AMNH (the other six were so damaged by shotgun pellets that we could not obtain a full set of measurements). In the graph of specimen scores projected onto the first and second principal components extracted from principal-components analysis shown in figure 32, scores for the four specimens from Bumbulan (indicated by delicate arrows) are clumped with scores representing squirrels from the central core of Sulawesi, the northern peninsula, and the northeastern arm.

The sample from Bumbulan does not depart in any significant way from the extent of variation in color of underparts and dimensions of the skull and tooth rows expressed by other geographic samples of *P. murinus*.

Prosciurillus abstrusus Moore, 1958

HOLOTYPE AND TYPE LOCALITY: The holotype of *Prosciurillus abstrusus* is an adult female (AMNH 101378) collected by Gerd Heinrich on January 4, 1932. A stuffed museum study skin and accompanying skull comprise the holotype. The skin is intact as is the cranium and the mandible; all teeth are present.

The type locality is Tanke Salokko, 1500 m, a high place on Pegunungan Mekongga, a mountain range in the southeastern peninsula of Sulawesi (see the maps and discussions in Heinrich [1932] and Stresemann [1940], and locality 1 in the gazetteer and map in figure 30), 03°35′S, 121°15′E (for the Pegunungan), Propinsi Sulawesi Tenggara, Indonesia.

EMENDED DIAGNOSIS: A small-bodied tree squirrel that in its morphology is most like *Prosciurillus murinus* among nannosciurine squirrels, but differs in having slightly duller upperparts and underparts, medial surfaces of the ears covered with white fur (but not extending beyond the pinnae rims to form tufts), absolutely larger skull, and relatively shorter rostrum but longer tooth rows (see section on comparisons).

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTION: This squirrel is known only from Pegunungan Mekongga where it was collected at 1500 m and 2000 m, elevations that bracket the transition between lower and upper tropical montane forest formations. Collections from lower elevations in tropical lowland evergreen rain forest in the foothills of Pegunungan Mekongga at 550 mm (Masembo) and on the coast 50 m (Wawo) between the Pegunungan and coast contained only *Prosciurillus murinus*.

Our knowledge of the montane fauna on Pegunungan Mekongga comes from the collecting efforts of G. Heinrich, his wife, and her sister at Tanke Salokko in 1932. Heinrich hunted birds and squirrels, his wife and sister trapped rats. Their samples of rats contained three species endemic to the mountain range and three others that are also found elsewhere. *Taeromys arcuatus* (collected at 1500 and 2000 m) and *T. microbullatus* (1500 m), along with *Rattus salocco* (1500 m), a member of the *Rattus xanthurus* group of species (Musser and Carleton, 2005), are, like the tree squirrel *Prosciurillus abstrusus*, endemic to the mountain range (Musser, MS). Samples of four other species of murid rodents—*Bunomys chrysocomus*, *B. penitus*, *Paruromys dominator*, and *Rattus hoffmanni*—were trapped at 1500 and 2000 m. *Bunomys chrysocomus*, *Paruromys dominator*, and *Rattus hoffmanni* also range into the lowland forests at the base of the Mekongga range and are found throughout Sulawesi; *Bunomys penitus* is restricted to montane forest habitats and also occurs on the western mountain block of Sulawesi's central core (Musser and Holden, 1991; Musser and Carleton, 2005; Musser, MS).

Maxomys dollmani is another rat found at Tanke Salokko along with *Prosciurillus abstrusus*. Unlike the tree squirrel, however, the distribution of *M. dollmani* extends to the central part of the west-central region in the central core of Sulawesi where it is represented by a single specimen (Musser, 1969). *Prosciurillus murinus* occurs throughout that western mountain block, but *P. abstrusus* does not.

DESCRIPTION: *Prosciurillus abstrusus* is one of the smallest-bodied of the species of

tree squirrels endemic to Sulawesi (length of head and body, 115–148 mm, length of hind foot, 35–38 mm; extremes from table 36), matched only by *P. murinus* in external dimensions (length of head and body, 102–150 mm; length of hind foot, 32–38 mm; extremes from table 36). The moderately thick coat (12–15 mm) clothing upperparts of head and body is dark brown flecked with pale buff; the ventral fur is dark grayish white with a pale buff wash over the chest on some specimens. The tail is shorter than the length of the head and body (LT/LHB = 81%) and the same color as the upperparts. Backs of the ears are densely covered with fine white hairs, forming a conspicuous white patch and providing the only contrast to the dark brown dorsum.

Females have three pairs of teats, one postaxillary pair and two inguinal pairs, the same combination possessed by all species of *Prosciurillus*.

Views of the small skull are illustrated in figures 12–14, where it is compared with skulls from other species of *Prosciurillus*; cranial and dental measurements are summarized in table 38.

COMPARISONS: *Prosciurillus abstrusus* is most closely related to *P. murinus* and the two species are contrasted in the account of the latter.

GEOGRAPHIC VARIATION: This aspect is not possible to document at the present time because samples of *P. abstrusus* have been collected at only two elevations in one small area (Tanke Salokko) of the elongate Mekongga range.

ECOLOGY: No information is available covering these topics. Elsewhere on mainland Sulawesi, 1500 m, the lowest collection locality for *P. abstrusus*, would be in lower montane forest and 2000 m, the highest place where the species was obtained, would mark the beginning of the upper montane forest zone.

ECTOPARASITES: The sucking louse, *Hoplopleura abstrusus*, n. sp., uniquely parasitizes *Prosciurillus abstrusus* (see descriptions of lice in the following section). Also, ectoparasitic laelapid mites were recovered from six *P. abstrusus* pelts (AMNH 101353, 101355, 101357, 101359, 101361, and 101363), all collected at Tanke Salokko, Pegunungan Mekongga in southeastern Sulawesi at an elevation of 2000 m in 1931.

SYMPATRY: *Prosciurillus abstrusus* is the only squirrel that has been collected from the high reaches of Pegunungan Mekongga (tables 3, 5). It is replaced at lower elevations by its close relative, *P. murinus* (see that account). The only other member of *Prosciurillus* recorded from the southwestern peninsula is *P. alstoni*, a member of the *P. leucomus* group of species. It has been collected in the foothills of Pegunungan Mekongga at Masembo (550 m) and Mowewe (500 m) and at lower elevations on the western coastal plain at Wawo (50 m) and Lalolei (300 m). Samples of both *P. alstoni* and the smaller-bodied *P. murinus* have been taken at Masembo and Waso.

The large-bodied *Rubrisciurus rubriventer* has also been collected on the southeastern peninsula. Specimens are from Masembo, Wawo, and Lalolei, and from the slopes of Pegunungan Mekongga at 600 m and 1400 m. Whether the altitudinal ranges of *P. abstrusus* and *R. rubriventer* overlap between 1400 m and 1500 m or the distribution is parapatric in pattern is unknown.

SYNONYMS: No scientific name has been applied to a sample of *P. abstrusus* in the context of identifying a separate taxon. As part of his report on relationships among living members of Sciurinae, which was based on a survey of cranial traits, Moore (1959: 203) listed a specimen of "*Prosciurillus obscurus*" used in his synoptic set of specimens. The individual (AMNH 101354) is an example of *P. abstrusus*, and "*obscurus*" was simply a lapsus; the name has no nomenclatural status except as a *nomen nudum*.

Hyosciurus Archbold and Tate, 1935

"On the basis then of the extreme length of the nasals of old adults, the shortness of the tail, the long narrow foot, and the pronounced elongation of the claws,—this last perhaps in relation to a shift from arboreal to terrestrial or even semi-fossorial habits—it has seemed advisable to set up a separate genus, which may be named *Hyosciurus*," was Archbold and Tate's (1935: 2) introduction to their description of this remarkable tropical ground squirrel:

> A callosciurine genus of squirrel in which the nasal part of the skull reaches an extreme degree of lengthening in the adult (length of nasals exceeds length of frontals); the transverse suture between frontals and parietals forms an irregular, backwardly bowed arch ...; nasals and premaxillae strongly produced in front of incisors; molar series carried forward so that the lacrimal is on a level with m^2 instead of m^1. Angular process of mandible strongly reflected. ... Hind foot not typical of the normal sturdy tree-squirrel foot, but long and slender, the width at the base of the 5th metatarsal only 7 mm. (about 14 per cent of foot length, excluding the claws). Claws very long and but little curved; those of the forefoot about 8 mm. (or 80 per cent of length of 4th digit); those of hind foot 7 mm. (nearly 60 per cent of length of 4th digit). Tail very short, from 50 to 70 per cent of length of head and body. Mammary formula not determined.

The holotype and two other specimens were collected by G. Heinrich from Pegunungan Latimojong in central Sulawesi (see gazetteer), and the species was named in his honor, *H. heinrichi*. Heinrich had also collected two long-nosed squirrels from Gunung Ile-Ile in the northern peninsula of Sulawesi and these were also identified as *H. heinrichi* by Archbold and Tate (1935). A year later, however, Tate and Archbold (1936: 1) described the sample from Gunung Ile-Ile under the name *ileile* and arranged it as a subspecies of *H. heinrichi*. The perception of one species of *Hyosciurus* with a subspecies occurring on the northern peninsula and another in the central core of Sulawesi persisted (Ellerman, 1940; Laurie and Hill, 1954) until Musser caught squirrels with both morphologies in the northern portion of central Sulawesi, *heinrichi* in the mountains and *ileile* in the lowlands with the two distributed parapatrically at middle elevations (Musser, 1987). Primary checklists of mammals published after 1987 have recognized the two species (Corbet and Hill, 1992; Hoffmann et al., 1993; Thorington and Hoffmann, 2005).

Archbold and Tate (1935) thought *Hyosciurus* to be structurally similar to the long-nosed *Rhinosciurus laticaudatus* found on the Malaya Peninsula, Sumatra, Borneo, and some smaller islands on the Sunda Shelf (Corbet and Hill, 1992: 302). Ellerman (1940: 398) also compared *Hyosciurus* with *Rhinosciurus* but at the same time signaled their trenchant cranial differences, and later, in his volume on additions and corrections to the 1940 treatise (Ellerman, 1949: 14), noted that:

> *Hyosciurus* further differs from *Rhinosciurus* in having a much shorter proportionate orbit length, which in *Hyosciurus* is below a quarter of occipitonasal length, as in *Nannosciurus*. This is interesting because all the Squirrels from Celebes I have seen except the large *Callosciurus rubriventer* have a tendency to shortening of the orbit, and it suggests that *Hyosciurus* is not closely allied to *Rhinosciurus*, but is derived probably from one of the more primitive Celebes Squirrels and has acquired its lengthening of the rostrum quite independently of *Rhinosciurus*.

Ellerman's view was supported by diagnostic cranial traits described by Moore (1959) that in his view consolidated the Sulawesian *Hyosciurus*, *Prosciurillus*, and *Rubrisciurus* into a natural group, the subtribe Hyosciurina of tribe Callosciurini; *Rhinosciurus* was placed in subtribe Callosciurina, which contained most of the other Indomalayan genera. For Moore (1959: 175), "Ellerman ... noted the important difference between *Hyosciurus* and *Rhinosciurus* and quite rightly inferred that they acquired their specializations of extremely long noses separately."

Other researchers disagreed. In the early 1940s, Zahn (1942: 116) promulgated the opinion, which was extreme at the time, that Sulawesian *heinrichi* was simply a species of Sundaic *Rhinosciurus*. In the 1990s, Zahn's assessment was given a degree of legitimacy, for Corbet and Hill (1992: 301) allowed that "*Hyosciurus* should perhaps be included" in *Rhinosciurus* and pointed out that both species of *Hyosciurus* (p. 302) "have the hair in the mid-line of the nape reversed, often followed by a median parting of hair, about 3–4 cm long, between the shoulders, a condition shared only by *Rhinosciurus* amongst Indomalayan squirrels."

Judged from analysis of molecular data, the shared protracted muzzle and reversed nape fur shared by *Hyosciurus* and *Rhinosciurus* do not signal close phylogenetic

affinity—but instead, independently acquired morphologies associated with the evolution of long-nosed ground squirrels in tropical Asian rain forests. Analyses of the nuclear IRBP and mitochondrial 12S and 16S ribosomal DNA used by Mercer and Roth (2003) recovered a squirrel phylogeny that included a monophyletic group containing *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* separate from a cladistic cluster formed by *Callosciurus*, *Rhinosciurus*, and their relatives (see section on classification). Within the Sulawesian clade, *Rubrisciurus* is more closely related to the species of tree squirrels in *Prosciurillus* than to the morphologically divergent ground squirrels in *Hyosciurus*. The results from this molecular inquiry unambiguously support the hypotheses presented by Ellerman (1949) and Moore (1959) and not the assessments of Zahn (1942) or Corbet and Hill (1992).

Previously published descriptions defining *Hyosciurus* are incomplete or inaccurate so we provide here an emended generic diagnosis. The following combination of traits will distinguish *Hyosciurus* from other nannosciurine genera (see comparative measurements summarized in table 3, and compare skulls illustrated in figures 6, 12–14, 36, 37): **(1)** diurnal and terrestrial; **(2)** elongate muzzle; **(3)** dark brown upperparts flecked with buff and black, without ear tufts, nape patches, or dorsal stripes, but with hair reversed on nape followed by a median parting for 10–40 mm; **(4)** underparts completely white or cream, or with white or cream swath marked by dark brownish gray strips and patches, or broken into segments separated by brownish gray ventral fur; **(5)** tail short, slightly less than half the length of head and body; **(6)** hind feet long and slender; **(7)** claws very long relative to length of foot (25%–35% the length of the front foot) and only slightly shorter than the digits, thin, and slightly curved; **(8)** three pairs of teats (one abdominal and two inguinal); **(9)** rostrum elongate, nasals longer than width of interorbital region, as long as frontals in *H. heinrichi* but shorter than frontals in *H. ileile* (nasals 83%–86% of length of frontals), nasals and premaxillaries project well beyond anterior faces of upper incisors to form a short tube; **(10)** orbit short (indicated by lacrimal and posterior margin of zygomatic plate even with second upper molar); **(11)** posterior processes of the frontals about even with posterior wall of suborbit (the space between postorbital process and braincase); **(12)** jugal component of zygomatic arch low relative to size of skull; **(13)** low temporal ridges meet and fuse in adults 3–5 mm before occiput to form a short and wide sagittal crest (about 15% of parietal length); **(14)** anterior opening of the infraorbital canal lies far posterior to the premaxillary-maxillary suture (a reflection of the protracted rostrum), is not concealed by a bony flange of the ventral zygomatic root, the anteroventral lip of the canal is thick (almost forming a large tubercle), and the outer surface rough for insertion of the superficial masseter; **(15)** no transbullar septa (see Moore, 1959); **(16)** pterygoid fossa narrow and shallow in *H. heinrichi*, its lateral margin outlined by a low, inconspicuous ridge (the "ectopterygoid ridge" of Moore, 1959, which he thought was absent from skulls of *Hyosciurus*); **(17)** posterior border of bony palate even or slightly posterior to caudal margins of third molars; **(18)** descending palatine vein typically transmitted through a foramen (posterior maxillary foramen) at the posterolateral margin of bony palate just caudad and slightly medial to end of tooth row; **(19)** braincase shorter relative to skull length (as measured by PPL/ONL: 40% for *Rubrisciurus*; 38%–40% for species in the *P. leucomus* group; 37% and 35% for *P. murinus* and *P. abstrusus*, respectively; 32% and 33% for *Hyosciurus heinrichi* and *H. ileile*, respectively; computed from means listed in tables of measurements); **(20)** upper incisors orthodont in configuration relative to the rostrum (emerging from the rostrum at a right angle); **(21)** maxillary tooth rows parallel; **(22)** third upper premolar present, fourth premolar and first and second molars wider (labial-lingual distance) than long (anterior-posterior length), third molar nearly circular in coronal view (about as wide as it is long).

Hyosciurus shares number of teats with *Prosciurillus* (both have three pairs, including two inguinal pairs, but the anterior pair is postaxillary in position in *Prosciurillus*, not abdominal as in *Hyosciurus*); a short orbit, parallel maxillary tooth rows, third upper

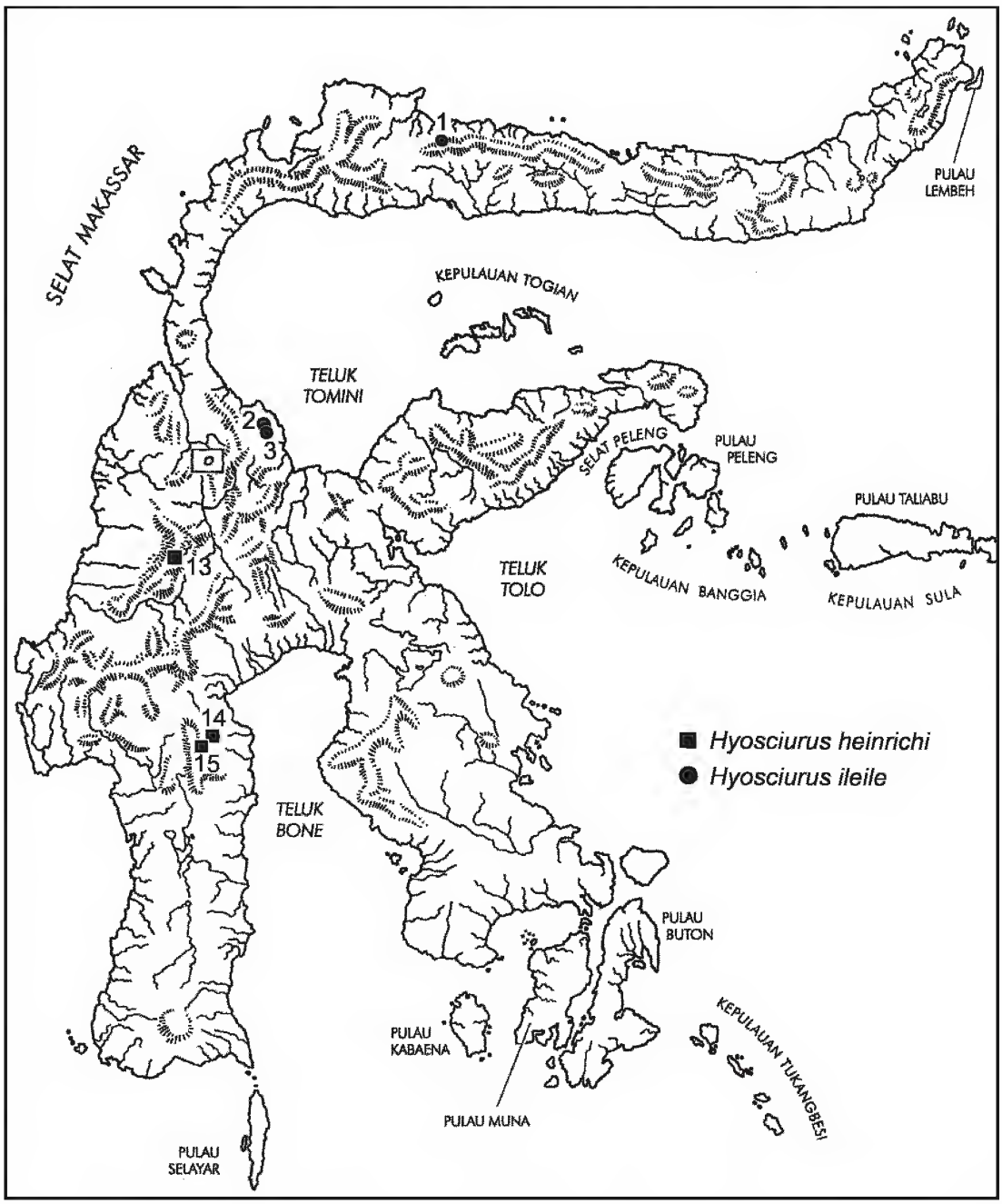

Fig. 35. Collection localities for samples of *Hyosciurus heinrichi* and *H. ileile*. Numbers key to localities described in the gazetteer where specimens are also identified by museum initials and catalog numbers. The inset map, right (rectangle in larger map, above), shows collection sites (1–12) for *H. heinrichi* scattered along Musser's transect over Gunung Kanino and Gunung Nokilalaki, and localities (4–9) for *H. ileile* lying along the Sungai Sadaunta and slopes of Gunung Kanino. The dashed contour line at 1300 m marks the approximate boundary between tropical lowland evergreen rain forest and tropical lower montane forest.

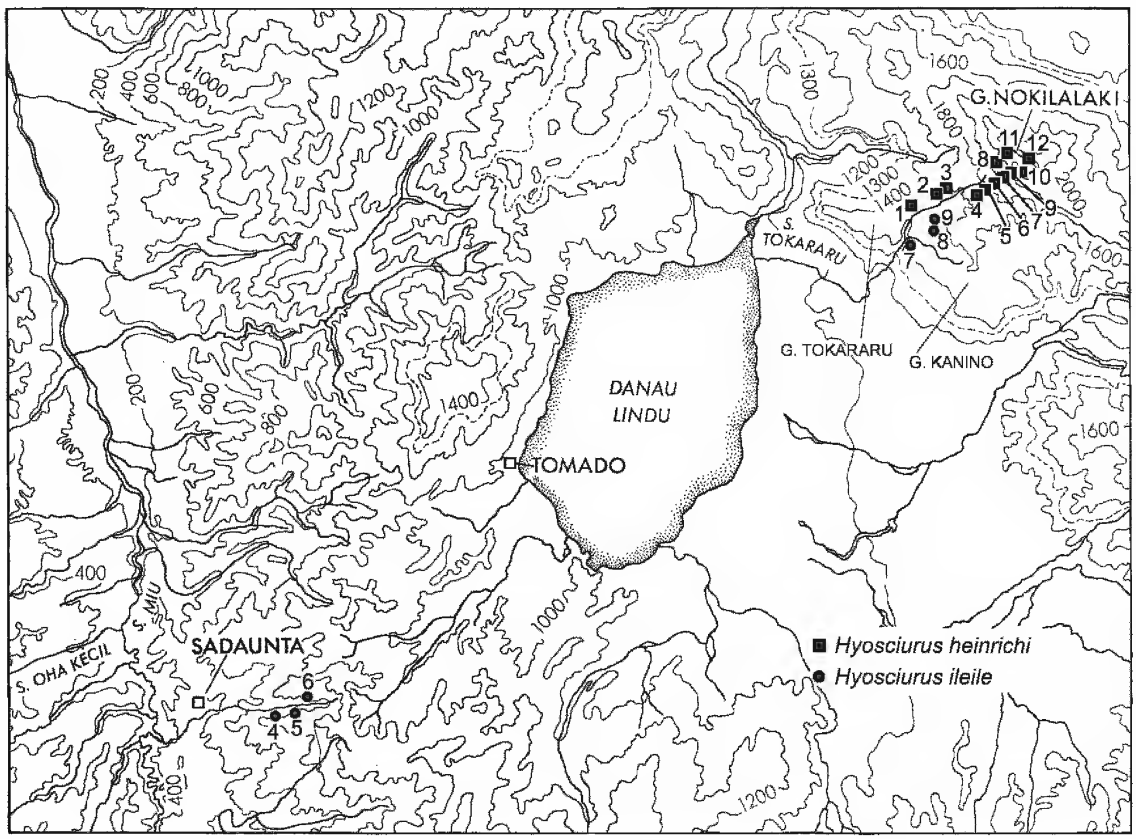

Fig. 35. *Continued.*

premolar, and fourth premolar and first and second premolars that are wider than long with both *Rubrisciurus* and *Prosciurillus*; the union of temporal ridges to form a sagittal crest anterior to the occiput with *Rubrisciurus* (but the temporal ridges are stronger, and the crest is longer in *Rubrisciurus*, forming one-third to three-fourths of the parietal length, depending upon age); and the position of the postorbital processes relative to the anterior margin of the braincase, and the relative size of the third molar with *Prosciurillus*. The combination of the other features in the diagnosis is unique to the Sulawesian ground squirrels.

Accounts of the two species of *Hyosciurus* are provided below. Qualitative morphological and quantitative morphometric comparisons between the two species are described and geographic and altitudinal distributions are outlined as derived from the collection localities of voucher specimens. The distinctiveness of the two species as defined by morphology and altitudinal distribution is supported by their sucking lice parasites. Each species of squirrel hosts a unique species of *Hoplopleura* (see the descriptions of sucking lice in the next section).

GAZETTEER AND SPECIMENS EXAMINED: Collection localities for the 53 specimens of *H. heinrichi* and the 14 examples of *H. ileile* studied are listed below. The number preceding each locality keys to a symbol on the map in figure 35.

Hyosciurus heinrichi

1. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 4850 ft (1479 m): AMNH 225483, 225484.
2. **Gunung Kanino**, 5040 ft (1537 m), AMNH 225485; 5100 ft (1555 m), AMNH 225486.
3. **Gunung Kanino**, 5150 ft (1570 m): AMNH 225487.

4. **Gunung Nokilalaki**, 01°13′S, 120°08′E, 5700 ft (1738 m): AMNH 223541.
5. **Gunung Nokilalaki**, 5800 ft (1768 m): AMNH 223543, 223545, 225598.
6. **Gunung Nokilalaki**, 6500 ft (1982 m): AMNH 225465.
7. **Gunung Nokilalaki**, 6800 ft (2073 m): AMNH 225466, 225467; 6850 ft (2091 m), AMNH 225468.
8. **Gunung Nokilalaki**, 7000 ft (2134 m): AMNH 225469.
9. **Gunung Nokilalaki**, 7200 ft (2195 m): AMNH 225470.
10. **Gunung Nokilalaki**, 7300 ft (2226 m): AMNH 223542, 224544, 223548, 225471.
11. **Gunung Nokilalaki**, 7400 ft (2256 m): AMNH 225472, 225473; 7450 ft (2271 m), AMNH 223551.
12. **Gunung Nokilalaki**, 7500 ft (2287 m): AMNH 223546, 223547, 223549, 223550, 225474–82.
13. **Pegunungan Takolekaju** ("Molengraff Range," the old European name for the mountain range, is notated on the specimen tags; no more precise collection locality is available; P. Jenkins, in litt., 2008), an extensive mountainous region in the western portion of the central core with the north-south boundaries between approximately 01° and 02°15′S, and extending slightly diagonally from about 119°45′E in the north to 120° near its southern ramparts, 4000–4300 ft (1220–1312 m): BMNH 40.641–40.652, 74.97.
14. **Pegunungan Latimojong**, 03°30′S, 121°23′E: 1600 m: AMNH 101311.
15. **Pegunungan Latimojong**, 2200 m: AMNH 101309; AMNH 101310 (holotype of *Hyosciurus heinrichi*), 196506.

We also examined BMNH 40.691b, 40.691c, and 40.691d from **Tamalanti** in Central Sulawesi, a place not indicated on the distribution map. Tamalanti, visited by the collector W.J.C. Frost in 1938, is a "Plantation between Rantekaroa [02°50′S, 119°50′E] and Koelawi [01°27′S,119°59′E]" (Laurie and Hill, 1954: 156), which was also the only information Musser and Paula Jenkins found when they searched through fieldnotes and other documents at BMNH. No elevation is notated on the specimen tags. Laurie and Hill (1954: 156) indicated that most of the animals collected by Frost at Tamalanti were recorded as coming from 3300–3800 ft (1006–1159 m), which seems too low for *H. heinrichi*.

Hyosciurus ileile

1. **Gunung Ile-Ile**, 00°58′N, 121°48′E (part of the larger Pegunungan Peleleh forming the mountainous backbone of the northwestern portion of the northern peninsula), 1700 m: AMNH 101308 (holotype of *Hyosciurus heinrichi ileile*), 196507.
2. Tolai, **Sungai Tolewonu**, 01°04′S, 120°27′E (estimated from Sheet SA 50-8), 550 ft (168 m): AMNH 226497.
3. Tolai, **Sungai Tolewonu**: 950 ft (290 m), AMNH 226498; 1100 ft (335 m), AMNH 226499.
4. Valley of Sungai Miu, **Sungai Sadaunta** (also spelled "Sidaonta" or Sidaunta"; tributary on right side of Sungai Miu), 01°23′S, 119°58′E (estimated from Sheet SA 50-8), 2900 ft (884 m): AMNH 224618.
5. **Sungai Sadaunta**, 3000 ft (915 m): AMNH 224619.
6. **Sungai Sadaunta**, 3150 ft (960 m): AMNH 224620.
7. **Gunung Kanino**, 01°17′S, 120°08′E (estimated from Sheet SA 50-8), 4600 ft (1402 m), AMNH 225459–62.
8. **Gunung Kanino**, 4800 ft (1463 m): AMNH 223540.
9. **Gunung Kanino**, 4960 ft (1512 m): AMNH 225463.

Hyosciurus heinrichi Archbold and Tate, 1935

Holotype and Type Locality: The holotype of *Hyosciurus heinrichi* is an adult male (AMNH 101310) collected by Gerd Heinrich on July 19, 1930. A stuffed museum study skin and accompanying skull comprise the holotype. The skin is intact as is the cranium and the mandible; all teeth are present (the skull, occlusal views of upper and lower cheek teeth, left dentary and right front foot are illustrated in Archbold and Tate, 1935: 3). Measurements are listed in table 42.

The type locality is Pegunungan Latimojong ("Latimojong Mts."), 2300 m, in the northern section of the southwestern peninsula (see the maps and discussions in Heinrich [1932] and Stresemann [1940], and locality 15 in the gazetteer and map in figure 35), 03°30′S, 121°23′E, Propinsi Sulawesi Selatan, Indonesia.

Emended Diagnosis: A ground squirrel distinguished from species of endemic tree squirrels in *Rubrisciurus* and *Prosciurillus* by the traits enumerated in the generic diagnosis. Morphologically similar to *Hyosciurus*

ileile but differs by having: **(1)** a much longer muzzle; **(2)** darker upperparts; **(3)** dark brownish gray underparts marked by a narrow midventral white swath with irregular borders that is broken up into white segments in some individuals; **(4)** slightly longer and thinner claws relative to size of feet; **(5)** larger ears but average shorter body, tail, and hind foot, as well as less mass; **(6)** much longer and slimmer rostrum; the tube formed by nasals and premaxillaries projecting farther beyond front faces of incisors; **(7)** longer nasals relative to length of frontals; **(8)** anterolateral rim of anterior opening of infraorbital canal slanted; **(9)** dorsal process of jugal lower, producing a more gracile zygomatic arch; **(10)** pterygoid fossae much narrower; **(11)** foramen ovale about twice as large; **(12)** posterior border of bony palate without a median projection in most specimens; **(13)** body of dentary slightly lower, posterior border between condyloid and angular processes more deeply concave. *Hyosciurus heinrichi* also differs from *H. ileile* in absolute means and proportions of the cranial and dental dimensions described in the section covering comparisons.

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: The latitudinal and longitudinal boundaries of *H. heinrichi* on Sulawesi are unknown, but the species may occur only in the mountainous west-central core of the island if the collection localities of voucher specimens reflect its real distribution (see gazetteer and map in figure 35). Samples come from the northern area (Gunung Kanino and Gunung Nokilalaki), the central region (Pegunungan Takolekaju and Tamalanti), and the southern highlands (Pegunungan Latimojong) of the western mountain block. The distribution of *H. heinrichi* in this western mountainous region of Sulawesi's central core is concordant with a suite of mammals—three species of shrews, at least two and possibly three tarsiers, a tree squirrel, and 14 species of murid rodents—that are so far known only from forest habitats in this region (table 25).

Elevational collection records that we judge to be reliable range from 1479 m in lower montane rain forest to 2287 in upper montane rain forest. This bracket contains elevations recorded by Musser on Gunung Kanino and Gunung Nokilalaki, and those made by Heinrich on Pegunungan Latimojong. W.J.C. Frost took specimens between 4000 and 4300 ft (1220–1312 m) on Pegunungan Takolekaju (Molengraff range),

TABLE 42
Age, Sex, and External, Cranial and Dental Measurements (mm) for Holotypes of *Hyosciurus ileile* and *Hyosciurus heinrichi*

Variable	*Hyosciurus heinrichi* AMNH 101310[a]	*Hyosciurus heinrichi ileile* AMNH 101308[a]
Type	holotype	holotype
Age	adult	young adult
Sex	male	female
LHB	211	205[213]
LT	104[105]	121[115]
LHF	51[54]	55[55]
LE	17.5	15
ONL	64.4	56.7
CBL	56.1	50.0
ZB	30.2	29.6
IB	15.4	14.7
LN	26.0	19.7
LR	35.4	27.3
BR	11.6	11.1
HR	9.9	10.4
MB	22.2	20.8
HBC	19.2	18.5
LO	11.7	12.0
LD	13.9	11.7
LBP	19.2	17.1
PPL	19.4	18.4
BBP	12.5	12.0
LB	9.2	9.2
CLPMM	10.0	10.3
LPT	10.2	7.8

[a]Values for lengths of head and body, tail, hind foot (excluding claws), and ear for the holotypes of *ileile* and *heinrichi* were obtained by G. Heinrich in the field; no specimens were weighed. Musser measured the dry hind foot (including claws) of each specimen (values in brackets). Heinrich measured each ear from crown to base, which produces a smaller value when compared to those obtained by measuring crown to notch (see table 43). Heinrich's values for lengths of head and body and tail are suspect. He had a tendency to include a portion of the rump in the tail measurement in some samples, but measured only the tail in other samples. Musser measured length of the dry tail of Heinrich's specimens, and values in brackets come from Musser's remeasurement of the dry tail and adding the difference between his and Heinrich's values to length of head and body (see table 43).

which is probably at the lower limit of lower montane rain forest. The three specimens collected by Frost from Tamalanti have no elevations recorded on the skin labels. Laurie and Hill (1954: 156) claimed that most of Frost's material from Tamalanti was obtained between 3300 and 3800 ft (1006–1159 m), but this range is within tropical lowland evergreen rain forest and too low for *H. heinrichi*, judged from Musser's experience with the species along his transect.

DESCRIPTION: *Hyosciurus heinrichi* is a moderately large, long-nosed, dark brown, and short-tailed ground squirrel (length of head and body, 195–240 mm; length of hind foot, 51–61 mm; weight, 228–370 g; extremes from table 43). Among the species of squirrels endemic to Sulawesi, *H. heinrichi* is slighter smaller than *H. ileile* and *Rubrisciurus rubriventer* in physical size but much larger than members of the *Prosciurillus leucomus* and *P. murinus* groups (table 3).

Chocolate brown fur flecked with buff and black covers the upperparts from the head to the base of the tail, including the ears, which lack tufts. The mix of dark gray wooly underhairs tipped with pale buff, longer overhairs that are dark gray or blackish along most of their lengths with a subterminal ochraceous or pale buffy band and black tip, and glistening black guard hairs combine to produce the lustrous dark brown cast to the pelage, which is also soft and dense (15–18 mm thick over the back). On the top of the neck just behind the ears the fur is reversed and then parted along the midline exposing the skin along a 30–40 mm strip. Each eye is surrounded by a hairless dark buffy ring. Dorsal surfaces of the front and hind feet are black to blackish gray, the palmar and plantar surfaces are black. Claws on the front digits are long, slim, and only slightly recurved (see the illustration in Archbold and Tate, 1935), 30%–35% of the length of the front foot (15%–20% for the much shorter and deeply recurved claws of the species of *Rubrisciurus* and *Prosciurillus*), and almost as long as the digits. Claws on digits of the hind feet are also slim and gently arcuate but are shorter (12%) relative to length of the foot.

Fur covering the underparts is white and dark grizzled brown in various patterns. Among the specimens from Gunung Kanino, Gunung Nokilalaki, Pegunungan Takolekaju, and Pegunungan Latimojong, the fullest expression is exhibited by five specimens: a pure white strip with ragged margins extends from the chin to the base of the tail and down inside each thigh (hairs are unpigmented for their entire lengths; the strip may appear cream on dry skins but is white on freshly caught squirrels). This midventral white swath is bordered by dark brownish gray ventral fur speckled with pale buff (hairs are very dark gray for most of their lengths and tipped with buff). The ventral region in the remainder of the sample of *H. heinrichi* can be sorted into five categories that roughly illustrate the nature of variation in venter pattern. **(1)** A white midventral strip extends from chin to groin, has uneven margins, and is broken up by a small dark brown midventral spot on the lower abdomen. **(2)** A white strip is interrupted by an elongate midventral dark brown patch on lower abdomen, and the grizzled brown of the abdominal margins protrudes into the white strip as round blobs on the upper abdomen and chest. **(3)** The white portion is reduced to a solid strip from the chin to upper abdomen where it splits into two white threads that bound a large midventral grizzled brown area, then rejoin to form a solid white expanse at the base of the tail. **(4)** The entire underparts are dark grizzled brown with a patch of white covering the chin, neck and chest, and another covering the inguinal region—the two white areas are separated by a expanse of grizzled brown; some specimens show a diffuse, wispy thread of white, interrupted in places, extending between the two solid white areas, and usually present only on one side. **(5)** Solid white covers the chin, throat, and chest, grizzled brown overlays the upper abdomen, and white covers the lower abdomen and inguinal region; the two solid white regions are wispily connected by a few white hairs along the midventral line through the brown area. From a solid white midventral strip (wide but not extending to lateral margins of the underparts) with uneven margins, the range of variation reflects a fracturing of that strip into white and brown areas by incursions to different degrees of the dark brown lateral margins of the venter fur.

TABLE 43

Descriptive Statistics for Measurements (mm) of Lengths of Head and Body, Tail, Hind Foot, and Ear, and for Weight (g) Derived from Samples of *Hyosciurus heinrichi* and *Hyosciurus ileile*[a]

Mean ± 1 SD, observed range (in parentheses), and size of sample are listed. Mean values were used to compute LT/LHB. Specimens measured are listed below.[b]

Variable	*H. heinrichi* central core (Gunung Kanino, Gunung Nokilalaki)	*H. heinrichi* central core (Pegunungan Latimojong)	*H. heinrichi* central core (Pegunungan Takolekaju)	*H. ileile* northern peninsula (Gunung Ile-Ile)	*H. ileile* central core (Sungai Sadaunta, Gunung Kanino, Sungai Tolewonu)
LHB	215.3 ± 8.82 (195–232) 35	212.5 ± 17.94 (197–238) 4	220.0 ± 11.08 (210–240) 12	200.5 ± 6.36 (196–205) 2 [222.0 ± 12.73] [213–231]	232.2 ± 9.74 (215–250) 11
LT	96.8 ± 11.15 (65–113) 35	99.5 ± 4.20 (95–104) 4 [99.3 ± 9.61] [85–105]	99.6 ± 14.57 (70–120) 11	127.0 ± 8.49 (121–133) 2 [106.5 ± 12.08] [98–115]	112.8 ± 15.28 (70–125) 11
LT/LHB (%)	45	47 [47]	45	63 [48]	49
LHF	55.7 ± 1.73 (52–61) 35	54.3 ± 0.96 (53–55) 4	54.3 ± 1.70 (51–57) 10	56.0 ± 1.41 (55–57) 2	58.4 ± 1.03 (57–60) 11
LE	23.6 ± 1.22 (21–26) 35	—	—	—	21.6 ± 0.51 (21–22) 11
WT	304.0 ± 39.67 (228–370) 35	—	—	—	395.6 ± 69.85 (293–520) 11

[a]Specimens of *H. ileile* from the central core and those representing *H. heinrichi* from Gunung Kanino and Gunung Nokilalaki were measured and weighed by Musser in the field (see Methods).

The holotype and other specimen of *H. ileile* from Gunung Ile-Ile were measured by G. Heinrich in the field, as were the holotype and additional three examples of *H. heinrichi* from Pegunungan Latimojong. He recorded total length along with lengths of tail, hind foot (excluding claws), and ear; no specimens were weighed. Musser measured the dry hind foot (including claws) of each specimen, which forms the basis of the statistics tabulated here for that variable. Heinrich's values for length of ear are excluded because he measured each ear from crown to base, which produces a smaller value (15 mm for each example from Gunung Ile-Ile, 17.5–18 mm for the four from Pegunungan Latimojong) when compared to those obtained by measuring crown to notch (Musser's endpoints). Heinrich's values for lengths of head and body and tail are suspect. He had a tendency to include a portion of the rump in the tail measurement in some samples, but measured only the tail in others. Musser measured length of the dry tail of Heinrich's material. The two sets of values are comparable for the sample from Pegunungan Latimojong (statistics derived from Musser's values for length of tail are in brackets), and the statistics are based on Heinrich's values, but strikingly dissimilar for the two skins from Gunung Ile-Ile. For the latter, the first set of statistics for lengths of head and body and length of tail are derived from Heinrich's values. Statistics in brackets come from Musser's remeasurement of the dry tail and adding the difference between his and Heinrich's values to length of head and body. The resulting means for each variable are more in line with those in the sample of *H. ileile* from the central core, as is the length of tail relative to head and body length (LT/LHB = 48%).

W.J.C. Frost measured specimens in the sample from Pegunungan Takolekaju (Molengraff range). Musser remeasured the dry hind feet and those values were used in the statistical calculations. Frost also measured length of ear, but from base to crown, not from notch to crown, and his values are less (15–18 mm for 12 specimens) than those obtained by Musser; we exclude analysis of his values for ear length. None of Frost's specimens were weighed.

[b]Gunung Ile-Ile: AMNH 101308 (holotype of *ileile*), 196507. Sungai Sadaunta: AMNH 224618–20. Gunung Kanino: AMNH 225459–63. Sungai Tolewonu: AMNH 226497–99. Gunung Kanino: AMNH 225483–487. Gunung Nokilalaki: AMNH 223541–549, 225464–82, 225598, 226550. Pegunungan Latimojong: AMNH 101309, 101310 (holotype of *heinrichi*), 101311, 196506. Pegunungan Takolekaju (Molengraff range): BMNH 40.641, 40.643–651, 74.97.

Slightly less than half the length of head and body (LT/LHB = 45%–47%), the tail is very dark brown with buffy and black highlights, coloration similar to the upperparts of the head and body.

Females have three pairs of teats: one abdominal pair (situated in the middle of the abdomen) and two inguinal pairs. The number matches that in all the species of *Prosciurillus*, but the most anterior pair is postaxillary in position in *Prosciurillus*, not in the middle of the abdomen. One or two young comprise a litter. No embryos were found in the few mature females examined, but one specimen had a placental scar in one uterine horn, and two squirrels had one scar in each horn.

Views of the elongate skull are illustrated in figure 36. Note the protracted rostrum and its prominent projection beyond the incisors, the moderately strong temporal ridges meeting to form a short sagittal crest, the short orbit, relatively low jugal component of the zygoma, postorbital process even with anterior surface of the braincase, position of the posterior margin of the bony palate relative to backs of the parallel tooth rows, very narrow ptergoid fossae bounded by a slight lateral ridge, spaceous foramen ovale, posterior maxillary foramen at each posterolateral margin of the bony palate, incisors emerging from the rostrum at a right angle (orthodont configuration), relatively smaller third upper molar, and slender but sturdy dentary. Cranial and dental measurements are summarized in table 44.

COMPARISONS: *Hyosciurus heinrichi* needs to be compared with the only other species in the genus, *H. ileile*. Both species share a similar physical build, but *H. heinrichi* is more gracile and less stocky than *H. ileile*, with a much longer muzzle. Typically, *H. heinrichi* has larger ears; a shorter body, tail, and hind foot; and weighs less (table 43).

The external dimensional contrasts are multivariately summarized in the ordination of scores projected onto the first and second principal components extracted from principal-components analysis illustrated in figure 38. The points form two clusters that barely overlap along the second axis but do so to a greater extent along the first component. The very high positive score for length of tail along with the lower and positive scores for length of head and body, and length of hind foot, contribute to the distribution of scores along the first axis (table 46), pushing the bulk of the scores representing specimens of *H. ileile* to the right of the *H. heinrichi* constellation, a reflection of the average greater lengths of these dimensions shown by *H. ileile* (table 43). Length of ear loads heaviest along the second component followed by length of head and body, and then length of hind foot. Clearly reflected here are the relatively much larger ears of *H. heinrichi* compared with *H. ileile*, and its relatively shorter body and hind feet.

Differences also exist between the two species in pelage coloration. Fur covering upperparts of head and body is dark brown flecked with buff and black in both species, but the coat of *H. heinrichi* is thicker, 15–18 mm as opposed to 10–12 mm in *H. ileile*, and appears slightly darker due to the longer, darker hairs. Fur on the neck just behind the ears is reversed followed by a part in both species, but the median part is 30–40 mm long in *H. heinrichi* and only 10 mm long in *H. ileile*. Coloration of the front and hind feet are similar in the two species although the palmar and plantar surfaces of *H. heinrichi* tend to be darker, black rather than slate gray as in *H. ileile*.

Color pattern of the ventral fur differs. It is dark grayish black speckled with pale buff on *Hyosciurus heinrichi* and marked by a midventral pure white region with irregular borders that is variable in coverage of the underparts. In its fullest extent, the white swath is moderately wide, but never covers the entire width of the underparts, and reaches from the chin to the base of the tail and inner surfaces of the thighs. Its weakest expression is a pattern where dark brown ventral fur covers the upper abdomen separating a white swath on the chin, throat, and chest from the white covering the lower abdomen and inguinal region (a detailed exposition of the range is provided in the section on description).

The entire venter, from the chin to base of the tail and inner surfaces of the thighs is cream-colored in *H. ileile*, not pure white as in *H. heinrichi* (Musser recorded this chro-

matic distinction in the field as seen on freshly caught animals). The cream swath covers nearly the entire venter and is bounded by even borders. On each specimen from the central core of Sulawesi and the two from Gunung Ile-Ile, the cream underparts are interrupted by a small midventral brown area. At one end of the variation of spotting in the samples from Musser's transect is a specimen that displays a small (5 × 10 mm) midventral spot between the thighs. At the other end is a squirrel with a thin midventral brown strip reaching from the abdomen to base of the tail. Of the rest of the specimens, one has two midventral brown spots on the lower abdomen, and the rest show a single brown blob (10 × 20 mm) in the middle of the lower abdomen. Among the two squirrels from Gunung Ile-Ile, the holotype has a narrow patch of midventral brown hairs on the lower abdomen (not obvious because the patch was sewn into the seam after the skin was stuffed), and a round brown incursion in the right postaxillary region. Lateral borders of the cream portion are uneven because of the uneven way the skin was sewn. The other specimen has a tuft of brown hairs in the inguinal region (partially concealed in the sewn seam). The range in patterning of the venter that is seen in *H. heinrichi* is not present in *H. ileile*.

Both species have long claws but those of *H. heinrichi* are slightly slimmer (more gracile) and longer relative to length of foot (30%–35% of front foot length in *H. heinrichi*, 25%–28% in *H. ileile*).

The majority of differences between the two species expressed in the skull reflect in *H. heinrichi* a greater specialization associated with the elongated rostrum and a less specialized conformation in *H. ileile*. The protracted muzzle of *H. heinrichi* compared to the shorter version typical of *H. ileile* extends to the cranial architecture (figs. 36, 37). Mean values of dimensions from the back of the skull—its breadth (indexed by MB), postpalatal region (PPL), breadth of the bony palate (BBP), and length of the tooth row (CLPMM)—are not significantly different in the two species (tables 44, 45). On the other hand, the mean values of dimensions describing the facial skeleton—lengths of the rostrum (LR), nasals (LN), diastema (LD), bony palate (LBP), and projection of the bony nasal tube beyond the upper incisors (LPT)—are much greater in *H. heinrichi* than in the sample of *H. ileile*, and the rostrum is not as deep (HR), reflecting the absolutely longer, slimmer, and more protracted rostrum of *H. heinrichi*, and its much longer extension beyond front faces of the incisors compared with the shorter and broader anterior half of the skull in *H. ileile*. Paralleling the longer rostrum of *H. heinrichi* is its longer skull (ONL, CBL). The skull of *H. heinrichi* is also typically narrower (narrower zygomatic breadth, ZB), with a narrower interorbital region (IB), shorter orbit (LO), shallower braincase (HBC), and much smaller ectotympanic bullae (LB) compared with those dimensions in *H. ileile*.

Qualitative contrasts involving the nasals, jugal, opening of the infraorbital foramina, bony palate, pterygoid fossa, foramen ovale, and dentaries also distinguish the two species. Nasals of *H. heinrichi* are about as long as the frontals, those of *H. ileile* are shorter than the frontals (83%–86% the length of the frontals). The jugal of *H. heinrichi* is low and the entire arch is gracile, while the jugal of *H. ileile* has a higher dorsal process and the arch appears more robust (not shown in the drawings as clearly as is seen on specimens). We did not measure jugal height but the contrast between the two species is evident when skulls are compared side-by-side. The lateral lip of the infraorbital canal is typically at a slant in *H. heinrichi* but vertical in *H. ileile*. Most specimens of *H. heinrichi* are without a conspicuous midventral posterior projection on the posterior margin of the bony palate (fig. 36); a very few display a midventral nubbin on the bony margin or a slightly larger bump. All the examples of *H. ileile* except the specimen portrayed in figure 37 have a prominent midventral process at the posterior margin of the bony palate. The pterygoid fossa in *H. heinrichi* is narrow, its lateral margin defined by an inconspicuous low ridge. *Hyosciurus ileile* has a much wider fossa, its surface triangular from ventral perspective, and marked laterally by a higher ridge; the shape, relative surface area of the fossa, and height of the bordering ridge form a configuration closely similar to that seen in the species of

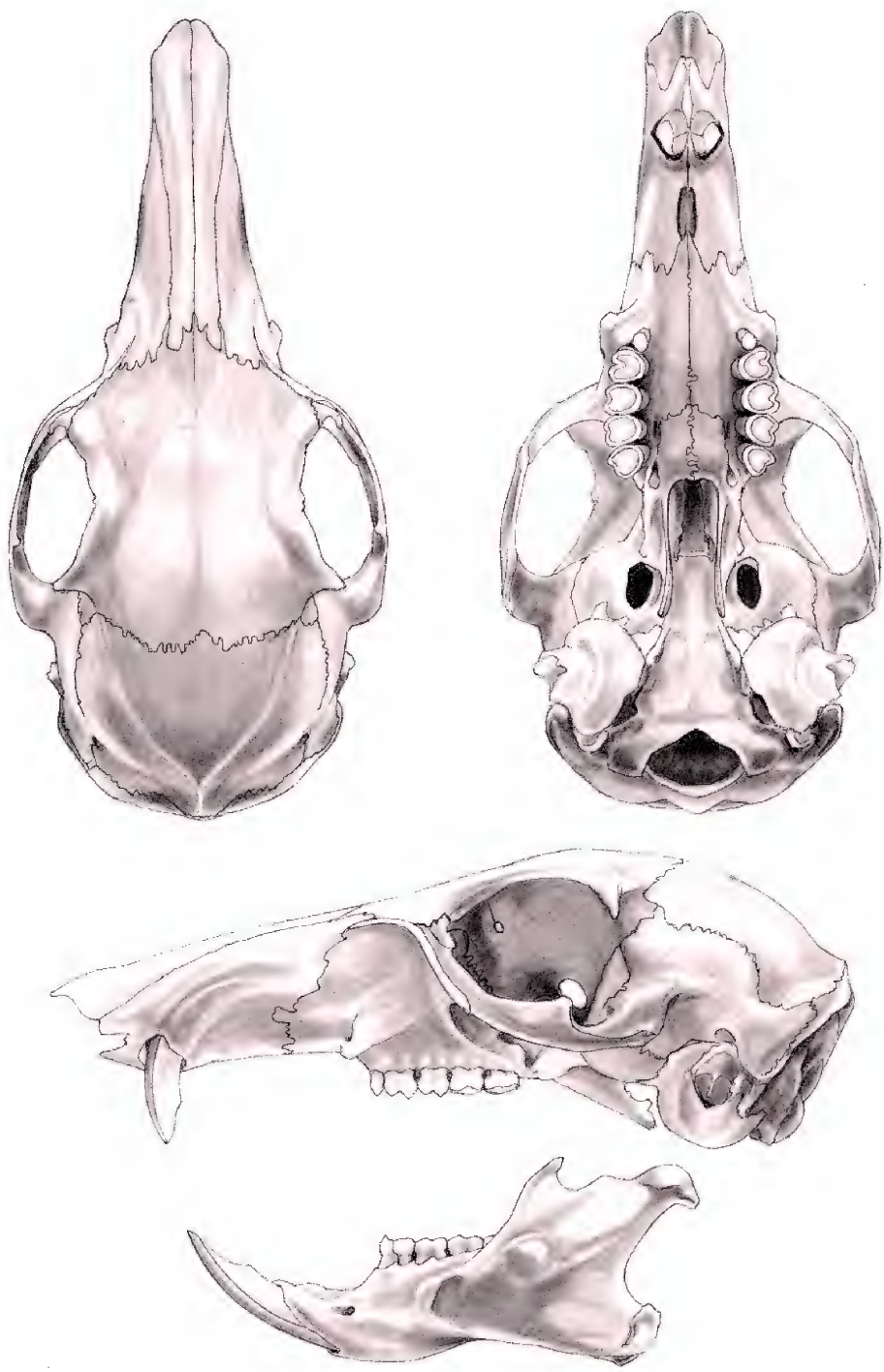

Fig. 36. Views of the skull and dentary of an adult male *Hyosciurus heinrichi* (AMNH 225478) from Gunung Nokilalaki (2287 m). Occipitonasal length = 64.9 mm.

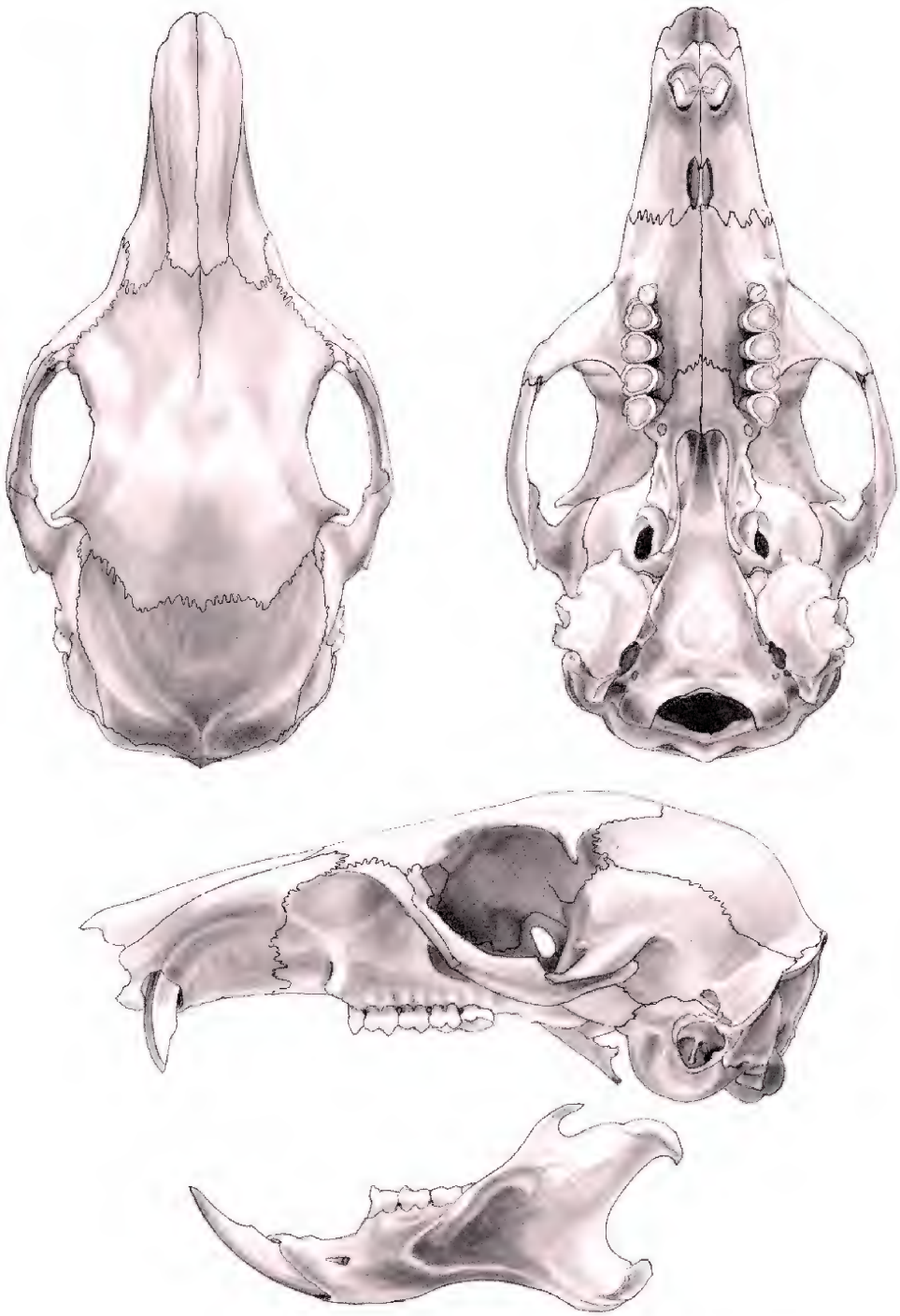

Fig. 37. Views of the skull and dentary of an adult male *Hyosciurus ileile* (AMNH 226498) from Sungai Tolewonu (290 m). Occipitonasal length = 63.1 mm.

TABLE 44
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of *Hyosciurus heinrichi*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Gunung Kanino $N = 5$	Gunung Nokilalaki $N = 17$	Pegunungan Latimojong $N = 4$	Pegunungan Takolekaju $N = 6$	Combined samples $N = 32$
ONL	63.6 ± 1.13	63.0 ± 1.30	63.9 ± 2.47	65.2 ± 1.71	63.6 ± 0.67
	(62.6–65.0)	(59.9–64.9)	(60.7–66.7)	(63.0–67.3)	(59.9–67.3)
CBL	55.9 ± 0.73	55.7 ± 1.29	55.1 ± 1.86	57.7 ± 1.58	56.0 ± 1.53
	(55.0–56.5)	(53.2–57.9)	(52.5–56.7)	(56.0–59.6)	(52.5–59.6)
ZB	30.6 ± 0.70	30.4 ± 0.87	30.1 ± 0.90	31.1 ± 0.84	30.5 ± 0.85
	(29.7–31.5)	(28.8–32.4)	(29.5–31.4)	(29.7–31.8)	(28.8–32.4)
IB	15.4 ± 0.49	15.2 ± 0.89	15.4 ± 0.33	15.9 ± 0.46	15.4 ± 0.74
	(15.0–16.2)	(14.2–16.3)	(15.0–15.8)	(15.2–16.4)	(14.0–16.4)
LN	25.2 ± 0.65	25.3 ± 0.82	26.1 ± 1.84	25.6 ± 1.35	25.4 ± 1.05
	(24.3–26.1)	(23.5–26.5)	(23.5–27.7)	(23.6–27.4)	(23.5–27.7)
LR	33.1 ± 0.93	32.9 ± 1.14	34.6 ± 1.37	34.8 ± 1.22	33.5 ± 1.37
	(32.2–34.1)	(30.2–33.7)	(32.6–35.5)	(33.1–36.0)	(30.2–36.0)
BR	11.3 ± 0.33	11.4 ± 0.32	11.6 ± 0.37	11.5 ± 0.35	11.4 ± 0.33
	(11.0–11.7)	(10.9–12.1)	(11.1–12.0)	(11.2–12.1)	(10.9–12.1)
HR	10.2 ± 0.15	9.7 ± 0.26	9.8 ± 0.27	10.6 ± 0.27	10.0 ± 0.43
	(10.0–10.4)	(9.3–10.2)	(9.4–10.0)	(10.2–10.9)	(9.3–10.9)
MB	23.2 ± 0.18	23.0 ± 0.54	22.3 ± 0.47	22.3 ± 0.68	22.8 ± 0.60
	(23.0–23.4)	(21.9–24.1)	(21.9–23.0)	(21.3–23.1)	(21.3–24.1)
HBC	18.5 ± 0.54	18.3 ± 0.45	19.0 ± 0.67	18.8 ± 0.38	18.5 ± 0.52
	(17.8–19.2)	(17.5–19.2)	(18.2–19.8)	(18.1–19.2)	(17.5–19.8)
LO	12.1 ± 0.42	12.0 ± 0.22	12.0 ± 0.54	11.2 ± 0.55	11.8 ± 0.48
	(11.4–12.5)	(11.5–12.3)	(11.6–12.8)	(10.3–12.0)	(10.3–12.8)
LD	13.6 ± 0.32	13.4 ± 0.47	13.8 ± 0.74	13.9 ± 0.54	13.6 ± 0.52
	(13.1–14.0)	(12.5–14.5)	(12.9–14.7)	(13.2–14.7)	(12.5–14.7)
LBP	17.8 ± 0.29	17.9 ± 0.47	19.5 ± 0.67	19.6 ± 0.64	18.4 ± 0.92
	(17.6–18.2)	(17.0–18.9)	(18.7–20.1)	(18.9–20.2)	(17.0–20.2)
PPL	20.5 ± 0.60	20.1 ± 0.80	19.1 ± 0.74	20.0 ± 0.83	20.0 ± 0.84
	(19.9–21.4)	(18.0–21.1)	(18.2–19.9)	(19.0–21.3)	(18.0–21.4)
BBP	12.3 ± 0.32	12.3 ± 0.42	13.1 ± 0.62	13.4 ± 0.42	12.6 ± 0.64
	(12.0–12.7)	(11.4–12.5)	(12.5–13.9)	(12.7–13.8)	(11.4–13.9)
LB	9.2 ± 0.22	9.1 ± 0.20	9.1 ± 0.13	8.8 ± 0.38	9.1 ± 0.27
	(8.9–9.5)	(8.8–9.5)	(8.9–9.2)	(8.2–9.4)	(8.2–9.5)
CLPMM	10.3 ± 0.32	10.2 ± 0.30	10.3 ± 0.36	10.7 ± 0.43	10.3 ± 0.38
	(10.0–10.8)	(9.5–10.6)	(10.0–10.7)	(10.2–11.2)	(9.5–11.2)
LPT	9.8 ± 0.45	9.6 ± 0.38	10.3 ± 0.47	9.5 ± 0.18	9.7 ± 0.44
	(9.1–10.2)	(9.0–10.3)	(9.9–11.0)	(9.3–9.8)	(9.0–11.0)

Prosciurillus (figs. 12–14). Each foramen ovale is spacious in *H. heinrichi*, about twice the size of comparable foramina in *H. ileile*. Finally, *H. heinrichi* has a slightly slimmer dentary as indicated by its lower ramus, and the posterior border between condyloid and angular processes is more deeply concave than the configuration in *H. ileile* with its somewhat deeper ramus and shallower posterior border.

Two widely spaced clusters contained in the ordination of specimen scores projected onto the first and second principal components extracted from principal components analysis in figure 38 mirror the cranial differences described above. The position of the *H. ileile* cluster to the left and the *H. heinrichi* group to the right along the first axis is influenced mostly by the high and positive loadings for lengths of nasals, rostrum, and

TABLE 45
Descriptive Statistics for Cranial and Dental Measurements (mm) Derived from Population Samples of *Hyosciurus ileile*
Mean ± 1 SD and observed range (in parentheses) are listed.

Variable	Gunung Ile-Ile $N = 2$	Sungai Tolewonu $N = 3$	Sungai Sadaunta $N = 3$	Gunung Kanino $N = 5$	Combined samples $N = 13$
ONL	57.2 ± 0.64 (56.7–57.6)	62.7 ± 0.38 (62.4–63.1)	60.1 ± 0.57 (59.5–60.6)	59.6 ± 1.74 (57.0–61.4)	60.1 ± 2.08 (56.7–63.1)
CBL	50.9 ± 1.20 (50.0–51.7)	54.4 ± 1.50 (52.9–55.9)	53.2 ± 0.69 (52.8–54.0)	52.9 ± 1.45 (51.1–54.7)	53.0 ± 1.61 (50.0–55.9)
ZB	30.4 ± 1.13 (29.6–31.2)	32.1 ± 0.62 (31.4–32.6)	31.1 ± 0.66 (30.5–31.8)	31.1 ± 0.77 (30.0–32.0)	31.2 ± 0.87 (29.6–32.6)
IB	15.6 ± 1.27 (14.7–16.5)	16.8 ± 0.81 (16.2–17.7)	16.3 ± 0.15 (16.1–16.4)	15.9 ± 0.29 (15.5–16.3)	16.2 ± 0.67 (14.7–17.7)
LN	19.5 ± 0.35 (19.2–19.7)	22.4 ± 0.15 (22.2–22.5)	21.4 ± 0.93 (20.4–22.2)	20.7 ± 1.59 (18.1–22.3)	21.1 ± 1.40 (18.1–22.5)
LR	27.5 ± 0.21 (27.3–27.6)	30.7 ± 0.42 (30.2–31.0)	29.6 ± 0.81 (28.7–30.3)	29.5 ± 1.18 (27.7–30.7)	29.5 ± 1.28 (27.3–31.0)
BR	11.4 ± 0.42 (11.1–11.7)	12.2 ± 0.44 (11.7–12.5)	11.3 ± 0.46 (10.9–11.8)	11.1 ± 0.62 (10.6–12.0)	11.5 ± 0.64 (10.6–12.5)
HR	10.2 ± 0.28 (10.0–10.4)	11.7 ± 0.15 (11.5–11.8)	11.4 ± 0.49 (10.8–11.7)	11.6 ± 0.48 (10.8–12.1	11.3 ± 0.63 (10.0–12.1)
MB	22.2 ± 1.91 (20.8–23.5)	23.1 ± 0.45 (22.7–23.6)	22.7 ± 0.23 (22.4–22.8)	22.5 ± 0.37 (22.0–22.8)	22.6 ± 0.71 (20.8–23.6)
HBC	18.6 ± 0.14 (18.5–18.7)	19.5 ± 0.44 (19.0–19.8)	19.0 ± 0.24 (18.8–19.3)	19.0 ± 0.31 (18.7–19.4)	19.1 ± 0.40 (18.5–19.8)
LO	12.1 ± 0.14 (12.0–12.2)	12.7 ± 0.15 (12.5–12.8)	12.1 ± 0.10 (12.0–12.2)	12.0 ± 0.11 (11.9–12.2)	12.2 ± 0.28 (11.9–12.8)
LD	12.1 ± 0.50 (11.7–12.4)	13.2 ± 0.15 (13.1–13.4)	12.3 ± 0.36 (12.0–12.7)	12.6 ± 0.39 (12.4–13.3)	12.6 ± 0.52 (11.7–13.4)
LBP	17.5 ± 0.57 (17.1–17.9)	18.4 ± 0.27 (18.2–18.7)	17.7 ± 0.36 (17.3–18.0)	17.9 ± 0.21 (17.7–18.2)	17.9 ± 0.42 (17.1–18.7)
PPL	18.8 ± 0.57 (18.4–19.2)	20.9 ± 1.05 (19.8–21.9)	20.6 ± 0.31 (20.3–20.9)	20.1 ± 0.74 (19.5–21.0)	20.2 ± 0.94 (18.4–21.9)
BBP	12.4 ± 0.50 (12.0–12.7)	12.8 ± 0.30 (12.5–13.1)	12.5 ± 0.15 (12.3–12.6)	12.6 ± 0.24 (12.3–12.9)	12.6 ± 0.29 (12.0–13.1)
LB	9.4 ± 0.28 (9.2–9.6)	9.6 ± 0.40 (9.2–10.0)	9.7 ± 0.15 (9.6–9.9)	9.7 ± 0.27 (9.5–10.1)	9.7 ± 0.28 (9.2–10.1)
CLPMM	10.5 ± 0.21 (10.3–10.6)	10.6 ± 0.40 (10.2–11.0)	10.4 ± 0.35 (10.0–10.7)	10.2 ± 0.31 (10.0–10.7)	10.4 ± 0.36 (9.2–10.1)
LPT	7.6 ± 0.28 (7.4–7.8)	8.6 ± 0.21 (8.4–8.8)	8.0 ± 0.47 (7.5–8.4)	8.0 ± 0.15 (7.8–8.2)	8.1 ± 0.42 (7.4–8.8)

diastema along with extent of the rostral projection beyond the incisors (table 47); the moderate but still positive loadings for lengths of skull and bony palate; and the moderate to high negative values for interorbital breadth, heights of rostrum and braincase, and lengths of orbit and bulla. Loadings for breadths of the braincase (mastoid breadth) and bony palate as well as lengths of the postpalatal region and tooth rows have a marginal effect on producing the two clusters along the first principal component. The pattern of scores in this principal-components ordination is a multivariate analytical summary of the cranial differences between the two species of *Hyosciurus* that is also expressed by mean values of cranial dimensions (tables 44, 45) and can be seen in the illustrations of skulls (figs. 36, 37): *H. heinrichi* has an appreciably longer and more slender rostrum, narrower interorbital region, shorter orbit, shallower braincase, and

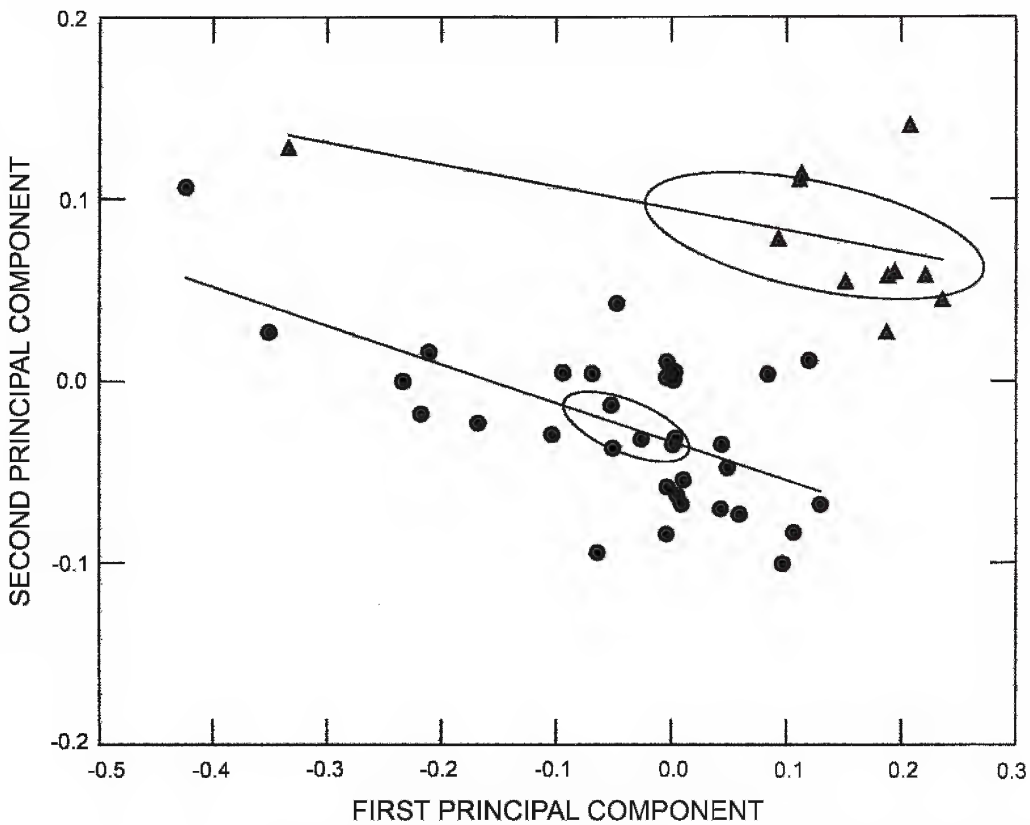

Fig. 38. Specimen scores representing population samples of *Hyosciurus heinrichi* (filled circle, Gunung Kanino and Gunung Nokilalaki; $N = 35$) and *H. ileile* (filled triangle, Sungai Sadaunta, Gunung Kanino, and Sungai Tolewonu; $N = 11$) projected onto the first and second principal components extracted from principal-components analysis. Each ellipse outlines 95% confidence limits for specimen scores of each cluster. Equations for the regression lines are: *H. ileile*, $Y = -0.121X+0.095$ ($F = 3.20$, $P = <0.10$); *H. heinrichi*, $Y = -0.213X-0.033$ ($F = 18.96$, $P = <0.001$). The regression lines of the second principal component on the first are unambiguously distinct: their Y-intercepts are significantly different (+0.095 versus −0.033; $F = 15.38$, $P = <0.001$), but not their slopes (−0.121 versus −0.213; $F = 1.16$, $P = 0.288$). The distribution of scores along the first axis is strongly influenced by length of tail, and the single point for *H. ileile* and the two for *H. heinrichi* situated far to the left of the main clouds of scores represent specimens with the shortest tails in the samples; the tails are naturally short, not damaged in traps or mangled by a predator and subsequently healed. Data were derived only from specimens captured and measured by Musser. See table 46 for correlations and percent variance.

smaller ectotympanic bullae compared with the cranial dimensions in *H. ileile*; skulls of *H. heinrichi* appear gracile, thin, and long, those of *H. ileile* appear stocky and short by comparison.

The bony mandibular architecture is similar in the two species (figs. 36, 37). The dentaries of each species are about the same length, but the body of the ramus is not as deep in *H. heinrichi* as it is in *H. ileile*, a distinction shown in the figures of skulls (we did not measure the mandibles).

Among the traits Tate and Archbold (1936: 1) used to separate *H. ileile* from *H. heinrichi* was the smaller third premolar ("a mere spicule") and first molar of *H. ileile* and its narrower pterygoid fossa (= mesopterygoid fossa). Of the two specimens in the type series from Gunung Ile-Ile, the holotype (AMNH 101308) has small, thin, and peg-like third premolars, and the other (AMNH 196507) has a small right third premolar, but lacks the left third premolar. Small to robust third premolars describes the range of

TABLE 46
Results of Principal-Components Analysis Contrasting Population Samples of *Hyosciurus ileile* with Those of *Hyosciurus heinrichi* from Central Sulawesi
Principal components are extracted from a covariance matrix of log-transformed values for lengths of head and body, tail, hind foot, and ear; see figure 38.

Variable	PC1	PC2
LHB	0.016	0.031
LT	0.148	−0.006
LHF	0.017	0.012
LE	−0.004	−0.052
Eigenvalues	0.022	0.004
Percent variance	76.2	13.0

variation in the series of *H. ileile* from the central core of Sulawesi, and a similar range in size occurs in our large sample of *H. heinrichi*. We detected no appreciable difference between the two species in size of the first molar or breadth of the mesopterygoid region; Corbet and Hill (1992) also did not appreciate the differences noted by Tate and Archbold.

GEOGRAPHIC VARIATION: Judged by head-and-body length, the specimens of *H. heinrichi* from Pegunungan Takolekaju average slightly larger than the series from Pegunungan Latimojong, Gunung Kanino, and Gunung Nokilalaki; however, absolute length of tail and tail length relative to body length, along with length of hind foot, are closely similar among all four geographic samples (table 43).

Color of the fur is comparable among the samples. All contain squirrels with chocolate brown upperparts and blackish feet. Underparts are white and blackish gray configured into a range of patterns as we described previously.

Mean values of cranial and dental dimensions reveal a picture of geographic variation that is summarized by the descriptive statistics listed in table 44 and results of multivariate analyses presented as specimen scores projected onto the first and second principal components extracted from principal-components analysis (fig. 39). Covariation in most variables influenced the spread of scores along the first axis (table 48), which reflects the greater size of certain dimensions in the sample from Pegunungan Takolekaju compared to the samples from Pegunungan Latimojong and from Musser's transect along Gunung Kanino and adjacent Gunung Nokilalaki. Mean values for some of the variables—length of skull and tooth row, breadth of the interorbital region, height of rostrum, and breadth of the bony palate—exceed those in the sample from Gunung Kanino and Gunung Nokilalaki (table 44).

Scores representing the four specimens from Pegunungan Latimojong fall between those from Musser's transect and the series from Pegunungan Takolekaju. The ellipses that outline 95% confidence limits for scores of specimens in each geographic sample indicate the relative homogeneity of the samples from Gunung Kanino and Gunung Nokilalaki (the former is a high ridge attached to the latter and unbroken montane forests cover both highlands), the separation of the Takolekaju sample from the Kanino-Nokilalaki specimens, and the intermediate position of the Latimojong series. This is somewhat surprising because Pegunungan Takolekaju lies between the highlands along Musser's transect and Pegunungan Latimojong, which is at the southern end of the mountains forming the western part of Sulawesi's central core (see map in fig. 35). Our analysis reveals variation in certain cranial dimensions among the three basic geographic samples—Gunung Kanino + Gunung Nokilalaki, Pegunungan Latimojong, and Pegunungan Takolekaju—with those from Musser's transect exhibiting the smaller skulls and those from Pegunungan Takolekaju the largest. What is the significance of these results? Does the variation in cranial and dental measurements among present samples simply reflect geographic variation due to differing intensities of gene flow among populations, or point to the Takolekaju sample as representing a population genetically isolated—or nearly so—from the other montane populations of ground squirrels? We do not know. Within a wide-ranging montane species like *H. heinrichi*, we would expect some morphometric variation from place to place, especially among highlands supporting montane forest habitats that are separated by major river valleys or lowland

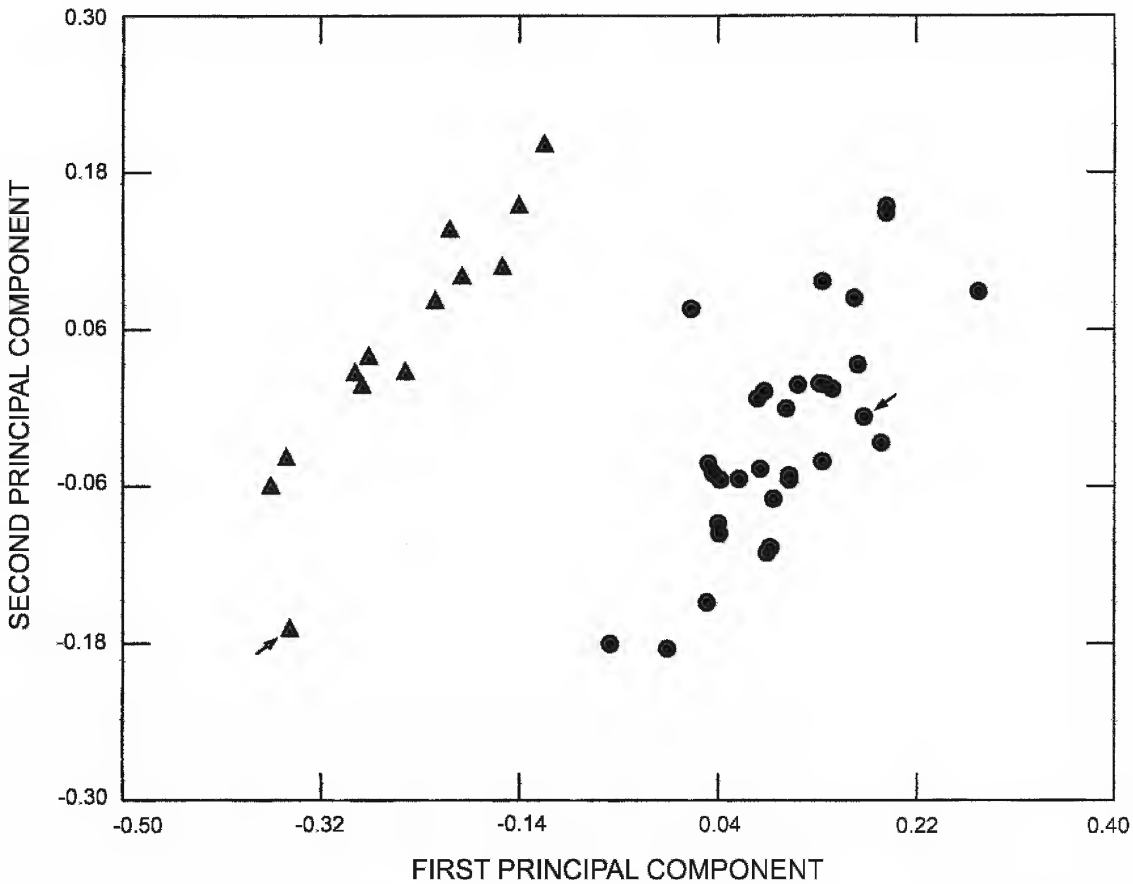

Fig. 39. Specimen scores representing four population samples of *Hyosciurus heinrichi* (filled circle, Gunung Kanino, Gunung Nokilalaki, Pegunungan Latimojong and Pegunungan Takolekaju; $N = 32$) and four population samples of *Hyosciurus ileile* (filled triangle, Gunung Ile-Ile, Sungai Tolewonu, Sungai Sadaunta, and Gunung Kanino; $N = 13$) projected onto the first and second principal components extracted from principal-components analysis. Arrows identify scores representing holotypes of *ileile* and *heinrichi*. See table 47 for correlations and percent variance.

evergreen rain-forest habitats. Uncovering existing patterns of genetic continuity or partial interruption among populations of *H. heinrichi* will depend on analyzing variation in external, cranial, and dental measurements among larger samples from more locations in the western mountain block south of Musser's transect. Compared with the large series from Gunung Kanino and Gunung Nokilalaki, there are only a few specimens in each of the samples from Pegunungan Takolekaju and Pegunungan Latimojong, and there are no specimens from montane regions between any of present collection sites. Fewer specimens per collection site would be required for extracting DNA samples, but broad geographic coverage would still be required.

In addition to the four geographic samples discussed above, a fifth, Tamalanti (see gazetteer), is closer to Gunung Kanino and Gunung Nokilalaki than to the other two collection sites; yielded three specimens that we did not measure because the skulls were incomplete or their condition otherwise unsatisfactory. During one visit to the British Museum, Musser compared the three skulls with his material and found them to be inseparable in overall size.

ECOLOGY: *Hyosciurus heinrichi* is terrestrial, diurnal, and inhabits cool and damp montane forests along streams, on hillsides,

TABLE 47
Results of Principal-Components Analysis Contrasting Population Samples of *Hyosciurus ileile* with Those of *Hyosciurus heinrichi*
Principal components are extracted from a covariance matrix of log-transformed values for 18 cranial and 1 dental variable; see figure 39.

Variable	PC1	PC2
ONL	0.035	0.015
CBL	0.032	0.015
ZB	−0.002	0.025
IB	−0.012	0.039
LN	0.098	0.002
LR	0.070	0.013
BR	0.005	0.013
HR	−0.043	0.055
MB	0.008	0.009
HBC	−0.007	0.018
LO	−0.008	0.007
LD	0.044	0.018
LBP	0.023	0.023
PPL	0.005	0.024
BBP	0.004	0.021
LB	−0.025	0.012
CLPMM	−0.002	0.016
LPT	0.089	−0.005
Eigenvalues	0.030	0.009
Percent variance	57.438	16.630

and on ridgetops (see table 2 where ambient temperature regimes are listed for Gunung Nokilalaki and Gunung Kanino). Musser worked only in primary forest on those highlands, so we do not know if populations of this ground squirrel can successfully inhabit second-growth forest or scrub habitats. On Gunung Nokilalaki, Musser caught the squirrels with Conibear traps placed in wide and prominent runways along the side of cut banks on steep slopes and along rock faces; beneath rotting, moss-covered tree trunks; under wet, mossy tangled trunks and limbs of rotting tree-falls; and among the mossy roots of rotting stumps and living trees (figs. 41, 42). Some of the runways ended in freshly dug burrows. In the vicinity of Gunung Kanino, Musser trapped the squirrels on tree trunks and limbs lying across the Sungai Tokararu (see trapping summary in table 49).

The furtive and quiet *H. heinrichi*, although common, is rarely seen in its dark and wet mossy forest habitat. Musser was fortunate to observe three individuals on the summit of Gunung Nokilalaki at 10:00 A.M. on a sunny day in April for about half an hour. At that spot the understory was open with scanty ground cover compared to the denser forest downslope where the thick understory made it nearly impossible to see the ground squirrels. Each of the squirrels was in the open, each had dashed from a runway, stopped in the clearing on a rock or raised point of ground, then dashed off again to disappear along or beneath a rotting tree trunk or stump and reappear again in the general vicinity. When running they appeared as long blackish streaks. At times each would stop, sit on its haunches, and twitch its tail much as all ground squirrels do, but never vocalize, then streak off and eventually disappear from sight. This was an exceptional encounter because squirrels were sometimes heard rustling through the undergrowth, but rarely seen.

A year later, on another April morning, Musser watched an individual for 10–15 minutes in a different area of forest on the summit of Nokilalaki. He stood about 10 ft from the squirrel, which was sitting on a rotting tree trunk covered with thick moss. From a distance, the squirrel resembled a round, dark brown ball of fur with a long face and big eyes. At first it responded to Musser's presence by leaping to the ground and scampering away for a few feet, but then returned to the top of the trunk to sit, occasionally grooming and biting ectoparasite-infested areas, scratching at other places in its fur, and sometimes chirping and sniffing about on the tree trunk. The squirrel kept its tail pressed closely to its back while sitting, jerking it along the back with every chirp. When the squirrel emitted a long series of calls, its tail would extend out behind the body; afterword, the tail reverted to its position against the squirrel's back. Often the squirrel would jump to the ground, scamper beneath the trunk where it remained for a minute or so looking over several old acorn husks, groom itself, and vocalize again. Once, after emitting a series of chirps it slowly approached Musser with nervous, jerky movements, stopping within 3 ft of him, and twitching its tail up and down before quickly scampering back to the trunk.

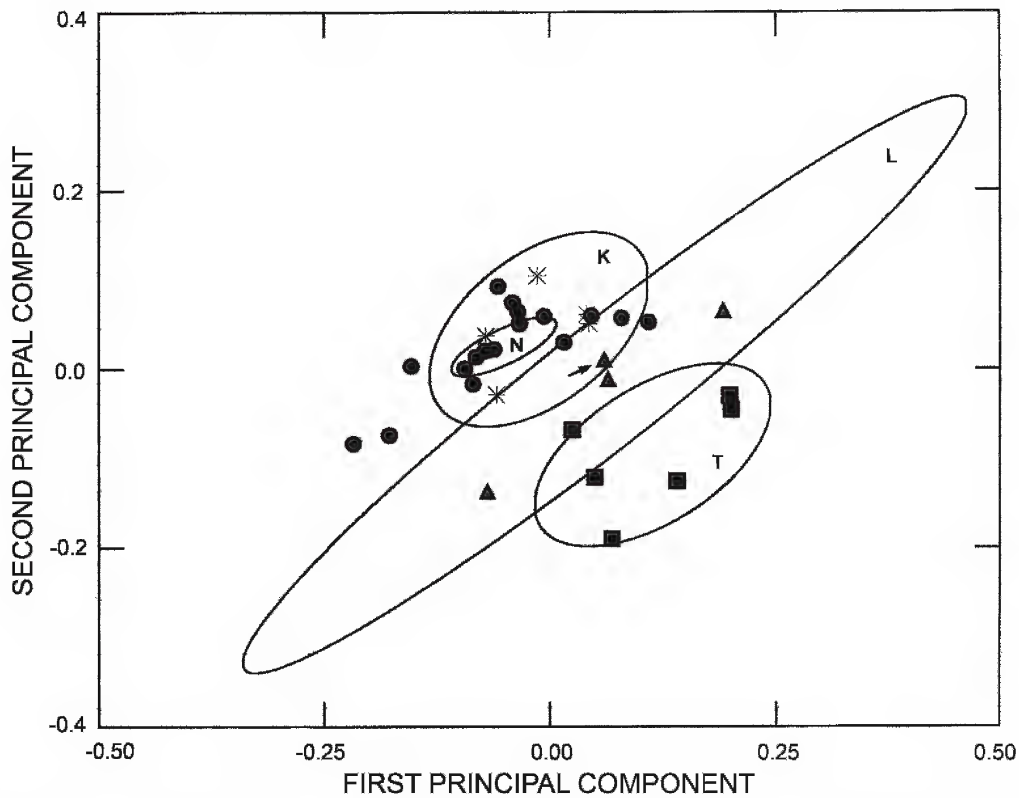

Fig. 40. Specimen scores representing four population samples of *Hyosciurus heinrichi* projected onto the first and second principal components extracted from principal-components analysis. Ellipses outline 95% confidence limits for scores of specimens from Gunung Nokilalaki (N, filled circle), Gunung Kanino (K, star), Pegunungan Latimojong (L, filled triangle), and Pegunungan Takolekaju (T, filled square). Arrow points to score for the holotype of *heinrichi*. See table 48 for correlations and percent variance.

Finally, Musser moved closer to the trunk, and the squirrel streaked away over the wet ground chirping continuously as it went, holding its tail straight behind its body.

The squirrel's voice was distinct from that of any species of the tree squirrels *Prosciurillus* and *Rubriventer* that Musser heard vocalize. As it sat, the ground squirrel uttered a string of single chirps, sounding more like a bird and not at all like a squirrel. When the squirrel became nervous or frightened, the calls increased in frequency and and the chirps had the slight suggestion of a chuck. Once or twice it became very agitated and chattered as most squirrels do, but the sounds were still soft, without the timber or resonance of the tree squirrels. Its bird-like vocalizations were deceptive, and as Musser worked daily in the forest, he did not know if the chirps heard most of the mornings issued from ground squirrels or birds.

Judged from contents of stomachs, the diet of *Hyosciurus heinrichi* consists of arthropods and some fruits, primarily acorns (fruit from species of *Lithocarpus*); see summary of stomach samples in tables 49 and 57. Some stomachs contained only arthropods, others arthropods and acorn mash, and a few were filled only with acorn mash. Geophilomorph and Scolopendromorph centipedes, the occasional ponerine and formicine ants and ant pupae, long-legged cursorial beetle larvae, several other kinds of beetle larvae with short legs, adult beetles, cockroaches, and certain kinds of fly larvae (Diptera) comprise an arthropod suite common to leaf litter (D. Grimaldi, personal commun., 2009). Another group of dipteran larvae found in stomachs,

TABLE 48
Results of Principal-Components Analysis Contrasting Population Samples of *Hyosciurus heinrichi*
Principal components are extracted from a covariance matrix of log-transformed values for 18 cranial and 1 dental variable; see figure 40.

Variable	PC1	PC2
ONL	0.024	0.005
CBL	0.022	0.006
ZB	0.020	0.006
IB	0.031	0.009
LN	0.031	0.014
LR	0.038	0.002
BR	0.005	0.002
HR	0.032	−0.012
MB	0.005	0.018
HBC	0.014	0.002
LO	−0.002	0.032
LD	0.033	0.010
LBP	0.040	−0.016
PPL	0.011	0.025
BBP	0.026	−0.036
LB	−0.003	0.018
CLPMM	0.019	−0.019
LPT	0.025	0.021
Eigenvalues	0.011	0.005
Percent variance	40.517	20.205

the Sciaroidea, live just below the ground surface and in wet moss; the female fly oviposits in the wet ground or moss below the surface and the eggs hatch into a ball of larvae. With its elongate muzzle and very long claws, the ground squirrel locates prey, then scratches and pokes through the leaf pack and moss (small segments of moss were found in stomachs) to pounce on any arthropods encountered. Exposing the subsurface soil environment with its long claws would allow the squirrel access to the larval Sciaroidea dipterans. In stomachs, this suite of leaf litter and subsurface arthropods were often contained in a clay-like ball separate from acorn mash. No stomach examined contained the large beetle larvae, usually legless, that live in rotting wood; such kinds of larvae were found in many stomachs of *Rubrisciurus rubriventer*.

The cranial architecture common to specimens of *H. heinrichi* exhibits adaptations well suited for procuring the dietary components found in contents of stomachs. A very long nasal region likely contains increased nasal epithelium that would enhance olfactory acuity. To a human, odors from wet soil, decaying leaf litter and rotting treefalls, and soaked moss saturate the air in mossy forest, and must be even more concentrated to a squirrel, which has better olfactory ability. Detecting dipteran larvae in wet ground and moss, and other arthropods within soaked and compressed leaf litter on the surface, probably requires heightened olfactory acuity that would cut through the prevailing ambient forest odors.

Opening acorns, a tough woody fruit, requires strong incisors along with forceful contributions from masseter and temporal muscles, and high premolars and molars affording surfaces for the mechanical breakdown of nuts over the squirrels' lifetime. Prominent temporal ridges meet in the midline near the occiput to form a short sagittal crest on the skull of *H. heinrichi*, the jugal component of each zygomatic arch is high, and the dentary elongate but robust; all provide firm origins and insertions for the array of masticatory muscles. This myological complex is joined by narrow but strong incisors, and large, high cheek teeth (fig. 36). Except for a shorter rostrum, the architecture is basically similar in *H. ileile* (fig. 37). The morphology contrasts sharply with that peculiar to the Indomalayan shrew-faced squirrel, *Rhinosciurus laticaudatus*, which has weak incisors that are very reduced in size relative to bulk of the skull, low cheek teeth that quickly wear to occlusal basins, slight temporal ridging extending to the occiput without forming a sagittal crest, low jugal, and delicate dentary (see illustration of skull in Corbet and Hill, 1992). Only arthropods and earthworms are eaten by this tropical ground squirrel (Davis, 1962; Medway, 1969; Payne et al., 1985), and that diet is reflected in the structure of its teeth and skull.

The small-bodied terrestrial shrew rat *Melasmothrix naso* occupies the same wet, mossy montane forest habitat as *Hyosciurus heinrichi*. With its long muzzle and claws, dark chestnut fur, short tail, and diurnal activity, the murid resembles a small version of the ground squirrel. *Melasmothrix naso* digs into the wet moss and ground for Sciaroidea dipteran larvae, but also eats

Fig. 41. Habitat of *Hyosciurus heinrichi* in upper montane rain forest on Gunung Nokilalaki, 2256 m. The tree squirrels *Prosciurillus topapuensis* and *P. murinus* also live here. The range of ambient temperatures recorded during the sampling period is listed in table 2. Photographed in 1975.

Fig. 42. Habitat of *Hyosciurus heinrichi* in upper montane forest on Gunung Nokilalaki, 2256 m. Traps set on top and beneath the rotting log in foreground took examples of *H. heinrichi*, which is common on the summit and upper slopes in this mossy, wet and cold forest. Photographed in 1975.

earthworms (Musser, 1982). No annelids were found in stomachs of the ground squirrel.

Stashes of empty acorn hulls are scattered through the montane forest beneath tree roots, rotting tree trunks lying on the ground, and tree holes just above ground. Many of the piles probably resulted from ground squirrel activities. Most of the empty hulls were in halves, some were mostly intact except for a small hole large enough to allow extraction of the seed. The ripe seed consists of a firm, white or gray endosperm enclosed by a thin brown seed coat. The squirrels eat the entire seed and it shows up in stomach samples as a semi-dry granular whitish or pale grayish mass (the endosperm) riddled with brown flecks (the seed coat).

Lithocarpus havilandii is the common oak in the mossy forest on Gunung Nokilalaki where older trees contribute to the canopy and younger trees and saplings are scattered throughout the understory. During December of 1973, acorns rained from the trees and littered the ground where they became forage for native pigs (*Sus celebensis*) and rodents. At lower altitudes in lower montane forest on Gunung Kanino, *L. glutinosus* and *L. elegans*

TABLE 49

Summary of Habitat at Trapping Sites, Stomach Contents, and Other Relevant Information for Specimens of *Hyosciurus heinrichi* Collected by Musser in Central Sulawesi, 1973–1975

Collection locality, specimen number, elevation, and month and year of collection are included. Descriptions of the trapping sites and contents of stomachs, slightly edited, are from Musser's field journals (in mammalogy archives at AMNH). Collection localities on Gunung Kanino are in lower montane rain forest, those on Gunung Nokilalaki are in upper montane rain forest. All squirrels were caught during the day in Conibear traps (rats taken in the same traps were caught during the night). Unless noted differently, trapping sites were in primary forest formations.

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
Gunung Kanino 225483 (3048)	1479	May 1975	On wet, decaying trunk (10 in. diameter) covered with thin layer of moss, lying 2 ft above water surface, crossing the Sungai Tokararu from one stream terrace to the other. **Stomach:** distended with acorn mash; no arthropod remains.
225484 (3053)	1479	May 1975	On decaying trunk (10 in. diameter), densely covered with wet moss, lying across Sungai Tokararu extending from a low terrace on one side of the stream a few inches above water level and crossing over stream to a higher terrace, 3 ft above water; no trails in moss, which is 1.5 in. thick and covers the entire trunk; also supports dense growth of epiphytes. This squirrel caught about 100 ft downstream from *Hyosciurus* ASE 3048, little change in altitude through this stretch of stream. **Stomach:** partially full, a bit of acorn mash and the rest remains of at least one large (2 in. long) chewed adult beetle.
225485 (3016)	1537	May 1975	On large rotting trunk (1 ft diameter) lying from stream terrace of the Tokararu across stream to opposite bank; terrace 3 ft high, thinly covered with wet moss, many ferns, young gingers, small plants, and young *Pandanus*. **Stomach**: full of acorn mash and arthropods (several small pomerine and formicine ants, several chewed geophilomorph and scolopendromorph centipedes, a small adult beetle, and remains of at least one cockroach—all leaf litter inhabitants).
225486 (3041)	1555	May 1975	On mossy trunk (4 in. diameter) growing horizontally across Sungai Tokararu about 1 ft above water level. **Stomach**: partially full, acorn mash, several whole and chewed geophilomorph centipedes, many chopped cursorial beetle larvae, a few dipteran larvae, and remains of small adult beetles.
225487 (3006)	1570	May 1975	On rotting trunk lying across Sungai Tokararu and 2 ft above water surface. Here the stream is about 4 ft wide, its cut bank is 8 ft wide and 2 ft high, and its terrace flat and 30 ft from slope to slope. Trunk (10–12 in. diameter) lies across terraces, is densely covered with thick moss (1 in. deep), from which are growing gingers, ferns, an oak-leaf fern, small shrubs, and tiny plants; no path is worn in moss. Terrace is wet and muddy, similar to that along the Sungai Salubeka where we were trapping *Hyosciurus ileile*. **Stomach**: distended with mostly acorn mash; mixed with it are chewed remains of several cursorial beetle larvae (with long legs) and another kind of beetle larvae (with short legs), fragments of small adult beetles, piece of geophilomorph centipede; the beetle larvae are the same kind as found in stomachs of *Hyosciurus heinrichi* caught at higher altitudes.
Gunung Nokilalaki 223541 (980)	1738	Dec. 1973	In prominent, wide runway beneath long, decaying moss-covered trunk decomposing on wet and steep forested slope; caught at 8:20 a.m.

TABLE 49
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
223790 (1057) 223965 (1070) 225465 (2563)	1768	Dec. 1973	In wide, damp and roofed runway beneath cut bank on steep slope just above camp. Runway is a tunnellike path extending along side of bank and leading into large alcoves eroded out from beneath tree roots. ASE 2563 was caught in February, its stomach was empty. Caught the rat *Bunomys penitus* in same spot as the three *Hyosciurus*.
225465 (2857)	1982	April 1975	In damp runway beneath section of rotting trunk covered with moss and shrubbery lying on side of ravine. Steep slope; trunk nearly concealed by dense undergrowth of shrubs and ferns.
225466 (2618)	2073	Mar. 1975	In damp runway (5 in. wide) alongside and partially under large decaying, wet, and moss-covered trunk lying on muddy slope between ridgetop and terrace; shrubby ground cover, dense rattan; always cool and wet here, sometimes flowing water just to one side of trap site. **Stomach**: full of acorn mash in which are mixed pieces of cursorial beetle larvae (with long legs), three other kinds of small beetle larva (with short legs), a few Sciaroidea dipteran larvae, a geophilomorph centipede, and bits of adult beetles.
225467 (2823)	2073	April 1975	In well-used runway beneath long, rotten and moss-covered trunk laying downslope about 20 ft from top of ridge; caught another *Hyosciurus heinrichi* on other side of ridge, also the rats, *Paruromys dominator* and *Rattus hoffmanni*. **Stomach:** partially filled with mostly acorn mash with fragments of at least one small adult beetle.
225468 (2888)	2091	April 1975	In runway alongside decaying, wet and moss-covered large and long section of trunk (2 ft diameter) lying in open ridge forest on steep slope 20 ft from top of ridge near where *Bunomys penitus* was caught. Scanty undercover. **Stomach**: full of mostly acorn mash mixed with a many chewed cursorial beetle larvae (with long legs) and a few of the short-legged beetle larvae, and fragments of adult beetles.
225469 (2593)	2134	Mar. 1975	On muddy ground next to face of boulder on wet slope; caught the rats *Bunomys penitus* and *Melasmothrix naso* in same spot. **Stomach:** partially full of some acorn mash, small geophilomorph centipede, a few cursorial beetle larvae (long, strong legs), another kind of beetle larvae (with tiny short legs), remains of adult beetles, and diptera larvae (Sciaroidea).
225470 (2898)	2195	April 1975	Trapped in wet runway alongside rotting, moss-covered section of trunk lying on side of muddy and rocky ravine. Caught the rat, *Rattus hoffmanni*, in same spot. **Stomach:** partially full of some acorn mash; abundant chewed pieces of cursorial beetle larvae (with long legs), a few examples of another kind of beetle larva (with short legs), some Sciaroidea dipteran larvae, and fragments from a few adult beetles.
223542 (1049) 223548 (1143)	2226	Dec. 1974	At base of moss-covered wet rock on steep slope below summit.
223544 (1069)	2226	Dec. 1974	In wet runway along base of wet, moss-covered rock under tree roots on nearly vertical slope below summit. Another *Hyosciurus heinrichi* was caught just across the trail in similar kind of runway.

TABLE 49
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
225472 (2838)	2256	April 1975	On ground in forest near where ASE 2256 was trapped. **Stomach:** distended, about half consisting of acorn mash and a lemon-tan fruit (smells fruity, not acorns), rest a muddy purple matrix packed with remains of at least two dozen large cursorial beetle larvae (more than seen in other stomachs).
225473 (2973)	2256	April 1975	In damp runway beneath roots of tall, old, live canopy oak growing on edge of ridge. Caught the rats, *Rattus hoffmanni* and *Melasmothrix naso*, in same area. **Stomach:** distended, 2/3 consists of acorn mash; rest is the muddy-purple paste containing two kinds of cursorial beetle larvae, remains of at least two kinds of adult beetles, and two large dipteran larvae (definitely associated with the purple mash and not the tan acorn mash).
223551 (1254)	2271	Dec. 1974	In wide, wet runway beneath rotting moss-covered trunk in wet forest.
225482 (2858)	2287	April 1975	In wide (8 in.), damp runway beneath long, rotting, moss-covered trunk (1.5 ft diameter) laying on muddy floor of short forest next to cement marker on summit. **Stomach:** full of acorn mash, no insect remains.
225474 (2619)	2287	Mar. 1975	In mossy, 6 in. wide runway beneath rotting, moss-covered trunk that is part of a large tangle of limbs, trunks, and branches from an old tree-fall lying amid thickets of ferns, sedges, gingers, and shrubs on steep slope below ridge summit. **Stomach**: filled mostly with acorn mash plus chewed remains of a few cursorial beetle larvae and adult beetles.
223546 (1113)	2287	Dec. 1974	Beneath a huge rotting trunk that forms the bottom of a tree-fall on summit; caught around 9:15 a.m.
223547 (1123)	2287	Dec. 1974	In damp runway beneath decaying, wet moss-covered trunk lying on ground at summit.
223549 (1175)	2287	Dec. 1974	In wet runway beneath a jumble of roots and trunks, all covered with thick and wet moss, lying on vertical side of summit in moss forest. The rat, *Rattus hoffmanni* was trapped in same spot.
226550 (1186)	2287	Dec. 1974	Beneath rotten, wet and moss-covered trunk lying on muddy ground at summit.
225475 (2630)	2287	Mar. 1975	In a classic runway (5–8 in. wide, tamped down, looking like a rat road) beneath a long, rotten, wet, and moss-covered trunk lying along a low hill just on edge of rolling, partially dissected terrain of ridge that forms summit. Runway extends entire length of trunk (30 ft), then through a pile of very rotten wood, and out into open where it can no longer be detected. The shrew rat, *Tateomys macrocercus*, was caught in same spot. **Stomach:** partially full of brown acorn mash, fragments of a few cursorial beetle larvae, and many Sciaroidea dipteran larvae.
225476 (2659)	2287	Mar. 1975	In wet runway (not mossy) beneath rotting, moss-covered, and wet trunk in forest on rolling edge of summit near cement marker. **Stomach**: full of mostly acorn mash discolored purple, abundant chewed remains of cursorial beetle larvae, and pieces of a small adult beetle.
225477 (2699)	2287	Mar. 1975	In wet runway running underneath a long rotten and thickly moss-covered trunk on side of the ridge a few feet below summit. **Stomach**: full of acorn mash; no insect remains.

TABLE 49
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
225478 (2713)	2287	Mar. 1975	In damp runway beneath long section of rotten, moss-covered trunk on hillside just below ridgetop near first grassy flat. **Stomach:** partially full of mostly acorn mash; remains of a large (2 in. long) adult beetle and a cursorial beetle larva.
225479 (2718) 225480 (2743)	2287	Mar. 1975	In wide runway beneath rotting, wet and moss-covered trunk on summit. **Stomach of ASE 2718** full: acorn mash, parts of beetles. **Stomach of ASE 2743**: full of dark gray ball of mud filled with remains of insect larvae (Sciaroidea dipteran larvae, indeterminate dipteran larvae, and cursorial coleopteran larvae) and a few geophilomorph centipedes. The cluster represents invertebrate fauna found in leaf litter covering the ground and soil just below ground surface. No fruit or acorn mash present.
225471 (2774)	2287	Mar. 1975	In wide earthen runway beneath jointed shrubs and rattan down from second grassy flat; caught during early morning hours, before 8:00. **Stomach**: full of acorn mash only; no invertebrate remains.
225481 (2775)	2287	Mar. 1975	Beneath exposed roots of three canopy-forming trunks coalesced at base, on steep slope just below top of ridge slightly beyond first grassy flat; earth is damp and tamped down beneath the roots. The rat, *Paruromys dominator*, was trapped in same spot but during the night. **Stomach:** full of acorn mash, no invertebrate remains. Large, live nematodes are present; nematodes were found in stomachs of all specimens of *Hyosciurus*.

replace the upper montane *L. havilandii*. In some places they are scattered through the forest on hillsides and ridgetops; in other areas they form large groves.

The fruit segment of the diet described here for *H. heinrichi* represents records for only part of a year. What fruits the squirrels may eat during other months, during the short dry season on the mountain, and at times when acorn production is unusually low, is unknown. Judged from stomach samples (table 49), fruit from oaks is preferred, but some unidentifiable fruit remains were present in a few stomachs. Fruit of chestnuts, *Castanopsis acuminatissima*, for example, may also be eaten. Groves of chestnuts intermingled with oaks and *Calophylum* are common on the upper slopes of Gunung Kanino and lower reaches of Gunung Nokilalaki to about 1800 m. Musser's observations contribute a degree of ecological information for *H. heinrichi*, but there is much more to learn about the ecology of this squirrel.

ECTOPARASITES: The sucking louse *Hoplopleura heinrichi*, n. sp. (see description in following section), uniquely parasitizes *Hyosciurus heinrichi*. The only other ectoparasite records consist of immature (larvae and/or nymphs) stages of hard ticks (Acari, Ixodoidea) belonging to the genera *Amblyomma* and *Haemaphysalis* (Durden et al., 2008; also see table 56 and ectoparasite account for *Rubrisciurus rubriventer*).

SYMPATRY: The range of *H. heinrichi* on the central core of mainland Sulawesi overlaps those of *Prosciurillus topapuensis*, *P. murinus*, and *Rubrisciurus rubriventer* (table 6). Along his transect in the northern portion of central Sulawesi, Musser trapped *H. heinrichi* in the same traplines that yielded the species of *Prosciurillus* and *Rubrisciurus*, and sometimes in the same traps (table 49).

Voucher specimens from collection sites along Musser's transect around Gunung Kanino indicate that in Sulawesi's central core *Hyosciurus heinrichi* and *H. ileile* are regionally sympatric but locally parapatric in

an elevational pattern where the lower border of the range of the montane species abuts the upper margin of the range for the lowland species. Musser never encountered the two species in the same trapline. The spatial relationship is roughly portrayed on the inset map showing the distribution of collection sites for each species (see fig. 35). From the southwestern side of Gunung Nokilalaki extends a high ridge that is bisected in the middle by a stream, the Sungai Tokararu (labeled on the map in fig. 4); the local people refer to the ridge on the west of the stream as Gunung Tokararu and that to the east as Gunung Kanino (both ridges are labeled on the inset map in fig. 35). The Tokararu originates below the summit of Nokilalaki, flows into a deep ravine along the northwestern margin of Gunung Kanino to pass through the cleft between the two ridges, and eventually empties into the waters of Danau Lindu. Musser worked on the top and upper sides of the Kanino ridge, on up to the summit of Nokilalaki on the eastern side of the Sungai Tokararu, and along the Tokararu stream at lower altitudes where it flowed alongside the Kanino ridge.

He collected *H. heinrichi* from the summit of Nokilalaki downslope east of the Tokararu to 1738 m, and along the Sungai Tokararu at the northwestern base of the Kanino ridge from 1570 m down to 1479 m (see gazetteer). He encountered *H. ileile* on the southeastern slope of the Kanino ridge just below the ridge-top and on the northwestern side just below the top of the ridge in a ravine containing the Sungai Salubeka, which is a small tributary of the Sungai Tokararu (and is drawn on the inset map in fig. 35 between localities 7 and 8, and labeled on the map in fig. 4); squirrels were trapped at 1512, m, 1463 m, and 1402 m, and encountered again along the Sungai Sadaunta below Danau Lindu between 884 m and 960 m.

In the Kanino area, the range of each species appears to reflect a parapatric pattern. *Hyosciurus heinrichi* was caught in the stream valley of the Tokararu at the base of the Kanino ridge and *H. ileile* was taken on the ridge itself just below the top (see tables 49 and 51 for habitats at each collection site). Parapatry may describe the ranges of the two species throughout the western mountains of the central core but no data are currently available to test this speculation. Both are similar in physical size, and both consume fruit, primarily acorns, and arthropods (see tables 43, 49, 51, and 57) and it seems unlikely that they would be found together at the same site. While samples of *H. heinrichi* have been obtained in the mountains south of Musser's transect (see gazetteer and fig. 35), no examples of *H. ileile* have ever been collected there, which may indicate its true absence but is more likely an artifact of trapping effort. Musser found *H. heinrichi* to be common in montane habitats and *H. ileile* to be uncommon wherever it occurred; short trapping periods (a few days) would produce the former but longer durations (months) and targeted trapping days would be required to sample the latter.

SYNONYMS: None.

Hyosciurus ileile Tate and Archbold, 1936

Hyosciurus heinrichi ileile Tate and Archbold, 1936: 1.

HOLOTYPE AND TYPE LOCALITY: The holotype of *Hyosciurus ileile* is a young adult female (AMNH 101308) collected by Gerd Heinrich (collector number 130) on November 21, 1930. A stuffed museum study skin and accompanying skull comprise the holotype. The skin is intact, as is the cranium with mandibles; all teeth are present. Measurements are listed in table 42.

The type locality is Gunung Ile-Ile, 00°58′N, 121°48′E (part of the larger Pegunungan Peleleh forming the mountainous backbone of the northwestern portion of the northern peninsula), 1700 m (see the maps and discussions in Heinrich [1932] and Stresemann [1940], and locality 1 in the gazetteer and map in figure 35), the extreme northwestern part of Propinsi Sulawesi Tengah, Indonesia.

EMENDED DIAGNOSIS: *Hyosciurus ileile* is most similar to *H. heinrichi* in morphological attributes, but differs in **(1)** its somewhat brighter upperparts; **(2)** typically mostly solid cream underparts; **(3)** shorter and blunter muzzle; **(4)** smaller ears; **(5)** heavier body and longer hind feet; **(6)** slightly shorter claws relative to size of feet; **(7)** shorter and more

robust rostrum; **(8)** shorter projection beyond incisor faces, and shorter nasals that are not as long as the frontals; **(9)** higher jugal that forms a more sturdy zygomatic arch; **(10)** higher and wider skull on average; and **(11)** different cranial proportions, as described in the account of *H. heinrichi* (see section detailing comparisons).

GEOGRAPHIC AND ALTITUDINAL DISTRIBUTIONS: The actual distribution of *Hyosciurus ileile* on Sulawesi is unknown. The few localities from which voucher specimens have been obtained include one montane area in the northwestern portion of the northern peninsula (Gunung Ile-Ile) and several places in the northern portion of the island's central core in tropical lowland evergreen and lower montane habitats (see gazetteer and map in figure 35). The species certainly has a broader distribution than present samples indicate, and should be sought elsewhere in the central core of the island, and on both the east-central and southeastern peninsulae. Its range on the northern peninsula most likely extends beyond Gunung Ile-Ile; we would expect to find the squirrel in landscapes throughout the western curve of the peninsula, from the Gorontalo region west to the base of the peninsula.

The range of *H. ileile* may not extend from Gorontalo east to the northeastern tip of the peninsula. This region was transformed into one or more islands during warm periods in the Pleistocene when sea level was considerably higher than at present (Fooden, 1969; Bintanja et al., 2005). Two species of macaques (*M. nigra* and *M. nigrescens*) and four murid species (*Echiothrix leucura*, *Taeromys taerae*, *Bunomys fratrorum*, and *Rattus xanthurus*) occur east of Gorontalo and have never been recorded from the northern peninsula west of the Gorontalo area (Fooden, 1969; Groves, 2005; Musser, MS). All these mammals have close phylogenetic relatives elsewhere on Sulawesi and their phenetic and genetic distinctiveness likely evolved from ancestral populations that were isolated on the northeastern Pleistocene islands. After Archipelago Sulawesi was transformed into its present-day configuration, some mammal species formerly occurring only in the western section of the northern peninsula and central part of the island may have gradually occupied habitats east of Gorontalo. Two species of murid rodents provide examples. *Bunomys chrysocomus* now occurs in forests throughout most of Sulawesi, including the northern peninsula where it is sympatric with *Bunomys fratrorum* in the region west of Gorontalo. *Rattus marmosurus*, a member of the *Rattus xanthurus* group (Musser and Carleton, 2005), is common in the central core of Sulawesi and also ranges through the northern peninsula where it can be found in the same habitat and altitude as the closely related *Rattus xanthurus* in the northeast. At least three species of shrews (*Crocidura nigripes*, *C. rhoditis*, and *C. elongate*), two tree squirrels (*Rubrisciurus rubriventer* and *Prosciurillus murinus*), and seven other species of murids (*Maxomys musschenbroekii*, *Maxomys hellwaldii*, *Lenomys meyeri*, *Margaretamys beccarii*, *Haeromys minahasae*, *Paruromys dominator*, and *Rattus hoffmanni*) occur in the central core of Sulawesi and on the northern peninsula east of Gorontalo. There is nothing in the morphology of specimens in samples of these species to suggest genetic isolation between populations in the central core and those on the eastern portion of the northern peninsula (this report; Musser, MS) and they may represent expansion from central Sulawesi into the northeastern peninsula after drops in sea level that exposed a connecting land mass covered in suitable forest habitats extending from the central core to the northeastern tip of intact Sulawesi. In contrast with these species, *Hyosciurus ileile* may have never dispersed east of the Gorontalo area. From the early days of Dutch occupation until the present, the northeastern Minahasa district has probably been the focus of more mammal collecting than any other region of Sulawesi, yet no samples of the ground squirrel have ever been obtained.

Gunung Ile-Ile at 1700 m is the highest site from which *H. ileile* has been collected and is in montane forest. In the central core of the island, 168 m to 1512 m are the elevational extremes documented by voucher material, and those samples came from a region of continuous forest cover extending from tropical lowland evergreen rain forest to lower montane rain forest.

The presence of *H. ileile* on the northern peninsula in montane forest at 1700 m, nearly 200 m higher than recorded in Sulawesi's central core, may reflect the absence of *H. heinrichi* from the peninsula. Present samples of *H. heinrichi* document its distribution in montane forest habitats, not in tropical lowland rain-forest habitats, and its parapatry with *H. ileile* at the lower boundary of its elevational range and the upper boundary limit of *H. ileile*. Both are ground squirrels, both are similar in body size and proportions, both exhibit similar pelage coloration, and both feed on *Lithocarpus* fruit and arthropods. This possible competitive altitudinal pattern should be the subject of careful ecological inquiries both on the northern peninsula and in the central core of the island.

DESCRIPTION: *Hyosciurus ileile* is of moderate size with a short tail (length of head and body, 215–250 mm; length of tail, 70–125 mm; length of hind foot, 57–60 mm; weight, 293–520 g; LT/LHB = 49%; extremes for sample from central Sulawesi extracted from table 43). It resembles *H. heinrichi* in physical build, but is larger and chunky in appearance with a shorter muzzle that appears blunt compared to the long face of *H. heinrichi* (photographs of a live *H. ileile* reproduced in figs. 43, 44). Upperparts show more brown tints, underparts are cream.

As in *H. heinrichi*, three pairs of teats are typical of *H. ileile*, one abdominal pair and two inguinal pairs. One female contained two embryos in a left uterine horn.

Views of the skull are provided in figure 37; compare these with those of *H. heinrichi* on the opposite page in figure 36. Cranial and dental measurements are summarized in table 45.

COMPARISONS: *Hyosciurus ileile* has been compared with *H. heinrichi* in the account of the latter.

GEOGRAPHIC VARIATION: We have two sets of samples for *H. ileile*. One consists of two very young adults (the type series) from Gunung Ile-Ile on the northern peninsula. The cheek teeth of both are slightly worn, and the presphenoid-basisphenoid and basisphenoid-basioccipital sutures are open. The other is composed of three samples from the northern part of Sulawesi's central core: three from lowlands in the Sungai Tolewonu region, three from Sungai Sadaunta, and six from Gunung Kanino (five were measured); very young adults, young adults, and adults are contained in these series. Specimens in both sets of samples resemble one another in body size and pelage coloration, except that the tails and hind feet of the two specimens from Gunung Ile-Ile average slightly shorter than those variables in the three samples from the central core of the island (table 43).

Some cranial dimensions are of comparable size in the two sets of samples (length of maxillary molar row, for example; table 45), but others are not. The two squirrels from Gunung Ile-Ile have a slightly shorter facial skeleton and basicranial region than do most of the specimens from Musser's transect. This contrast is reflected in mean values for dimensions related to the muzzle (length of nasals, LN; length of rostrum, LR; projection of nasals and premaxillary beyond the incisors, LPT; and height of rostrum, HR) and back of the skull (postpalatal length, PPL) that are listed in table 45, and the scatter of specimen scores projected onto the first and second principal components extracted from principal-components analysis displayed in figure 45. Covariation in nearly all cranial variables contributes at some intensity to the spread of scores along the first axis, an estimate of increasing size from left to right; especially forceful are the variables associated with length of the muzzle and back of the skull (table 50). Scores for the two squirrels from Gunung Ile-Ile lie on the left, and all but one of the scores representing specimens from the central core are scattered to the right. Of the five scores representing specimens from Gunung Kanino, a single very young adult (AMNH 225549: showing slight wear on the premolars and molars, and open presphenoid-basisphenoid and basisphenoid-basioccipital sutures) clusters with the two points for the squirrels from Gunung Ile-Ile.

Impressive variation in skull size exists within a particular age group, at least in those samples collected along Musser's transect (Sungai Tolewonu, Sungai Sadaunta, and Gunung Kanino). For example, of the 10 skulls measured for the principal-components analysis, five are adults and five are young

adults (all have slight wear on the occlusal surfaces of the cheek teeth and the basioccipital-basisphenoid suture and basisphenoid-presphenoid suture are completely open). The largest of the young adults has a skull length of 62.4 mm (AMNH 226497), the smallest is 57.0 mm (AMNH 225459). Skulls from the two squirrels collected on the northern peninsula on Gunung Ile-Ile are closely similar to AMNH 225459 in overall size and general conformation.

To reduce the effect of the adult specimens in the principal-components analysis, we eliminated them and employed only the two young adults from Gunung Ile-Ile and the five young adults from Musser's transect. The pattern of scores within the ordination defined by first and second principal components (not illustrated) is similar to the spread shown in figure 45 that was derived from young adults, adults, and old adults.

Whether the distribution of specimen scores derived from the available material reflects regional variation in cranial dimensions between samples from the northern peninsula and those from Sulawesi's central core, variation concomitant with age, or different gene pools is unclear. We have only two young squirrels from one montane locality at 1700 m on the northern peninsula, and 12 specimens from the central core collected through a range from 168 m to 1512 m. We know nothing about the characteristics of *Hyosciurus* that may inhabit forests between these sampled regions. Is the montane population of *H. ileile* on Gunung Ile-Ile characterized by small physical build or are we just seeing the very young adult end of the age spectrum? Is *H. ileile* restricted to montane habitats on the northern peninsula or does it range into tropical lowland evergreen forests on that peninsula? If *H. ileile* does inhabit lowland forests on the peninsula, are the phenetic and genetic attributes of these lowland squirrels the same as those in Sulawesi's central core? Or would genetic discontinuity exist between the lowland populations somewhere near the base of the northeastern part of the peninsula and the central core, a break coinciding with that between the tree squirrels *Prosciurillus leucomus* (peninsular distribution) and *P. topapuensis* (central core) and macaques *M. hecki* (peninsular) and *M. tonkeana* (central core)? Additional and larger samples from both the northern peninsula and the central core are required to answer these questions that bear on unraveling the possible significance of the morphometric variation we document among the present geographic samples.

ECOLOGY: *Hyosciurus ileile* is diurnal and terrestrial. In the northern part of central Sulawesi, the ground squirrel occurs throughout a range of forest habitats, from the warm and humid lowland tropical evergreen rain forests (environments similar to those shown in figs. 8, 22, and 23) to the cooler lower montane forests (fig. 27; see table 2 for ambient temperatures recorded at various camps through this range of habitats). The squirrels were trapped in streamside habitats and in forests on hills and ridgetops (see table 51 for a summary of habitats at trapping sites). Musser worked in the forest nearly every day at camps scattered from the lowlands to higher altitudes, but outside of those in traps saw the ground squirrel only once, near Tomado. He trapped 12 *H. ileile* at localities far apart along his transect; by contrast, twice as many *H. heinrichi* were encountered and within a relatively much smaller area on the transect line. Similar trapping regimes were employed everywhere along the transect.

That is why the following particular capture was a pleasant surprise. Musser recorded observations of an adult male *H. ileile* livetrapped on February 14, 1976, along the Sungai Tolewonu at 152 m. This handsome, beautiful squirrel was at first very nervous when caged, but soon grew accustomed to the enclosure, bumping and biting the sides only if unduly disturbed. He was active during the day, vocalizing in the morning and late afternoon; at night he slept curled on his side on a platform.

This individual's vocalization was unlike that of *H. heinrichi* and consisted of two different calls. When disturbed, or when he grabbed a beetle larva from Musser's fingers, he would growl "Errr, errr, grrr" in short bursts from deep within his throat; the tree squirrel *Rubrisciurus rubriventer* growls in a similar way. The only other type of call Musser heard was usually made in mornings and afternoons: a high-pitched squeal, "eeee,

Fig. 43. An adult male *Hyosciurus ileile* caught at 155 m above camp on the Sungai Tolewonu in tropical lowland evergreen rain forest. The squirrel was trapped on a large decaying trunk (2 ft in diameter) forming a bridge 15 m long straddling the river, one end on a narrow bank at base of steep hillside, the other resting on river terrace 3 ft above the water surface; caught about 10:30 a.m. See account of this species for description of behavior and diet. See table 2 for range of ambient temperatures recorded during the trapping duration at the Sungai Tolewonu. Photographed in 1976.

eeee," each squeal lasting 3–5 seconds. A variant was a drawn out single "eeee----e" that started high and dropped to silence, and a double "ee, ee" uttered quickly. All these kinds of squeals resembled the whine of an unoiled machine.

The squirrel quickly learned to drink water through a spout from a bottle, which he used throughout the day. Musser provided him with bait (a ground mixture of rolled oats, raisins, peanut butter, and bacon), nutmeg and ginger fruit, other kinds of fruit that are regularly eaten by *Rubrisciurus rubriventer*, small adult carabid beetles, small lizards, and earthworms. All were ignored. The only items accepted were large beetle larvae that

Fig. 44. A closer look at the squirrel shown in figure 43, just as it was fleeing the confines of the cage.

Musser excavated from rotting trunks and limbs lying on the forest floor, and acorns (fruit from *Lithocarpus*). The squirrel would grab the larva from Musser's hand, grasp it between his front feet, and proceed to eat the head, then open the thorax and consume the internal organs, but discard the soft abdomen. Adult beetles found in the same rotting wood as the larvae were offered to the squirrel but were ignored.

Musser cut open acorns from the two species of oak growing in the Tolewonu area to determine which species the squirrel preferred. *Lithocarpus celebicus*, the more common of the two, is a tall canopy tree, or sometimes an emergent, occurring on flat, damp river terraces and hillsides above the river, and here and there on higher slopes below ridgetops. This species was seen only in tropical lowland evergreen rain forest between 30 and 1000 m along Musser's transect. The other oak, *Lithocarpus glutinosus*, was less frequently encountered, growing on hillsides but apparently absent from wetter areas along stream terraces. Musser identified this species along his transect all the way up to Gunung Kanino. Most of the opened acorns from *L. celebicus* contained pulp and a small seed. The squirrel grabbed each opened section and quickly ate the seed, then gouged out and ate some of the pulp, but left most of it. Then he was given acorns from *L. glutinosus*, each of which was packed with a solid nutty seed covered with a very thin pale brown skin, with no pulp at all. The squirrel quickly took them and ate all the contents leaving only the hard husks. He clearly recognized the fruit and ate it voraciously, holding the acorn with his front feet and using the lower incisors to scoop out

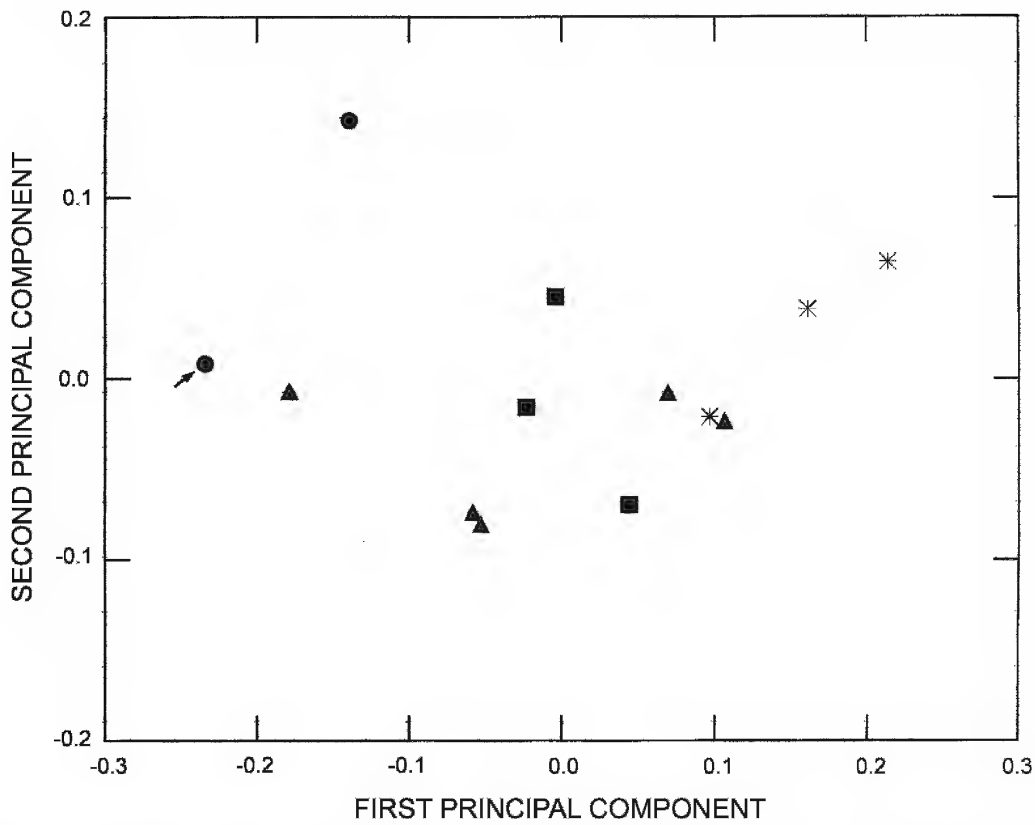

Fig. 45. Specimen scores representing four population samples of *Hyosciurus ileile* projected onto the first and second principal components extracted from principal-components analysis. Symbols identify scores for specimens from Gunung Ile-Ile (filled circle), Sungai Tolewonu (star), Sungai Sadaunta (filled square), and Gunung Kanino (filled triangle). Arrow identifies score for the holotype of *ileile*. See table 50 for correlations and percent variance.

the contents. The squirrel sat on his haunches as he ate the seed, with his tail curled against his back.

The squirrel was released a few days after capture; he jumped from cage to ground, poked about the camp for a few minutes, and finally fled into the forest uttering a low and guttural series of chucks as he disappeared from sight into the undergrowth.

Hyosciurus ileile, like its montane relative *H. heinrichi*, is a consumer of fruits and arthropods (tables 51, 57). Acorns (*Lithocarpus* fruits) and figs seem to be preferred, but other kinds of fruits with large seeds are also taken—the variety of fruits consumed is greater than that of *H. heinrichi*, at least judged by our samples. Remains of pill bugs (Crustacea, Isopoda), Geophilomorph and Scolopendromorph centipedes, scorpions, orthopterans, occasional ants, ant pupae, adult beetles, and large, long-legged cursorial beetle larvae were found in stomachs, pointing to leaf litter habitats on the ground surface as the source of prey.

The question of why *H. ileile* seems to be uncommon within its range compared to *H. heinrichi* needs to be addressed in future ecological studies. Relative abundance of oaks in tropical lowland evergreen rain forest as opposed to montane forests may be one of several factors responsible. Musser, in the process of collecting botanical samples, observed that oaks in the lowlands were widely scattered throughout the forest, usually single trees here and there, occasionally in small groves of three to four trees.

TABLE 50
Results of Principal-Components Analysis Contrasting Population Samples of *Hyosciurus ileile*
Principal components are extracted from a covariance matrix of log-transformed values for 18 cranial and 1 dental variable; see figure 45.

Variable	PC1	PC2
ONL	0.034	−0.001
CBL	0.029	0.001
ZB	0.025	0.004
IB	0.028	0.016
LN	0.060	−0.008
LR	0.041	−0.010
BR	0.038	0.036
HR	0.040	−0.037
MB	0.021	0.010
HBC	0.016	0.001
LO	0.016	0.009
LD	0.033	0.004
LBP	0.017	0.003
PPL	0.042	0.000
BBP	0.014	0.003
LB	0.011	−0.005
CLPMM	0.014	0.020
LPT	0.037	−0.010
Eigenvalues	0.018	0.004

Although *L. celebicus* was seen more frequently than *L. glutinosus*, neither of the two was common.

Oaks are more abundant in lower and upper montane forests and at least three species are present. Between 1400 and 1700 m on ridgetops and hillsides of Gunung Kanino and the lower slopes of Gunung Nokilalaki, *L. glutinosus* and *L. elegans* occur with chestnuts (*Castanopsis acuminatissima*) to form extensive groves in which some other trees are intermingled (*Calophylum*, for example). Those two oaks are replaced by *Lithocarpus havilandii* on higher slopes and the summit of Gunung Nokilalaki where it comprises one of the most common components of the forest, even forming extensive groves in places.

Both species of ground squirrels consume oak fruit and arthropods found in leaf litter (see table 57). Within the context of the distribution of oaks described above, population size of *H. ileile* in lowland forests may be constrained by the lower abundance of oaks compared to their higher abundance in montane forest habitats. These observations represent unquantified anecdotal information, but provide a hypothesis that could be tested by results from careful ecological inquiries.

Gunung Ile-Ile or elsewhere in Pegunungan Peleleh, which forms the mountainous backbone of the northwestern portion of the northern peninsula, would be an ideal place for a transect study extending from the lowlands into the mountain forests. *Hyosciurus ileile* has been taken in a high montane habitat; presumably it also occurs at lower altitudes down through tropical lowland evergreen rain forest, and present data indicate *H. heinrichi* is absent from the northern peninsula. In the absence of *H. heinrichi*, is the population size of *H. ileile* greater in the montane habitats and reduced in lowland forests? And along such a transect line, does the relative abundance of oak species resemble that observed by Musser in the central core of the island?

ECTOPARASITES: In addition to a host-specific sucking louse, *Hoplopleura ileile*, n. sp., this ground squirrel is parasitized by immature stages (larvae and/or nymphs) of ticks (Acari, Ixodidae) belonging to the genera *Dermacentor* and *Haemaphysalis* (Durden et al., 2008; also see table 56 and the ectoparasites account for *Rubrisciurus rubriventer*). Further, ectoparasitic laelapid mites were recovered from pelts AMNH 223540 and 225460, both from Gunung Kanino in central Sulawesi at elevations of 1402 and 1463 m in the 1970s.

SYMPATRY: The range of *H. ileile* on the northern peninsula of Sulawesi overlaps the ranges of *Prosciurillus leucomus*, *P. murinus*, and *Rubrisciurus rubriventer* (table 6). On Sulawesi's central core, the range overlaps those of *P. topapuensis*, *P. murinus*, and *R. rubrisciurus* (table 6). Along his transect in the northern portion of central Sulawesi, Musser trapped *H. ileile* in the same traplines, and sometimes in the same traps, as *P. topapuensis*, *P. murinus*, and *R. rubrisciurus* (table 51). See the account of *H. heinrichi* for the topographic relationships between the geographic and altitudinal distributions of *H. ileile* and *H. heinrichi*.

SYNONYMS: None.

We leave our accounting of Sulawesi's endemic species of squirrels and turn to

TABLE 51

Summary of Habitat, at Trapping Sites, Stomach Contents, and Other Relevant Information for Specimens of *Hyosciurus ileile* Collected by Musser in Central Sulawesi, 1974–1976

Collection locality, specimen numbers, elevation, and month and year of collection are included. Descriptions of the trapping sites and contents of stomachs, slightly edited, are from Musser's field journals (in mammalogy archives at AMNH). Two collection localities (Sungai Sadaunta and Sungai Tolewonu) are in tropical lowland evergreen rain forest. Sites on Gunung Kanino are in lower montane rain forest. All squirrels were caught during the day in Conibear traps (rats taken in the same traps were caught during the night). Unless noted differently, trapping sites were in primary forest formations.

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
Sungai Sadaunta 224618 (2225)	884	Oct. 1974	On decaying, wet *Pigafetta* palm trunk lying across stream in intact streamside forest. Three rats were trapped on same spot during different nights: two *Echiothrix centrosa* and one *Taeromys callitrichus*. **Stomach**: full of two kinds of figs (skin, rind, large and tiny seeds), brown acorn mash, hard pieces resembling a calyx, and soft green pieces, along with a few cut pieces of large beetle larvae, several young instar beetle larvae (with legs), and remains of an adult beetle.
224619 (2348)	915	Nov. 1974	On limb of understory tree growing across ravine containing main upper tributary of the Sungai Sadaunta; base of the trunk is at edge of stream, with the trunk leaning over the water and its upper branches reclining on the opposite terrace. The main connecting limb (3–5 ft in diameter) on which the trap was placed is mossy, and the moss is trampled, indicating frequent use; trap set about 7 ft from stream level. Examples of three kinds of tree squirrels (*Rubrisciurus rubriventer*, *Prosciurillus topapuensis*, and *P. murinus*) and an arboreal rat (*Rattus marmosurus*) were taken in the same spot. So three tree squirrels, one ground squirrel, and at least one species of arboreal murid used the same living pathway as a bridge over the stream. **Stomach**: full, with hard seeds covered by tissue (resembling seeds from the tall ginger but smaller and capsule shaped), remains of a cockroach and adult beetle, and several large long-legged cursorial beetle larvae (large pinkish orange larval abdomens, most without head and thorax, and part of thorax with legs of one larva).
224620 (2293)	960	Nov. 1974	On rotting trunk lying across high (3 ft) banks of main upper tributary of Sungai Sadaunta. Trunk covered with moss, ferns, and shrubs at either end, but clear in middle. Here sides of the canyon are steep, the ravine heavily eroded and cluttered with rotting *Pigafetta* palm fronds—these palms are common. Rattan is thick in understory of hillside and terrace forest above. Trees seem short, forest smaller than at 2500 ft. Caught during early morning. **Stomach**: full, mostly remains of large long-legged cursorial coleopteran, fragments of adult beetles (including wings), and some unidentifiable fruit mash.

TABLE 51
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
Guning Kanino 225459 (2531) 225460 (2532) 225461 (2537)	1402	Feb. 1974	On understory tree growing from one bank of Sungai Salubeka out over stream to other bank, main trunk about 4 ft above water. Tree is densely leaved; branches, twigs, and leaves nearly hidden by hanging, wet moss. Trunk is covered with moss that is beaten down along the top as though used often by animals to cross the stream. ASE 2531 caught during the day between 10:00 and 12:00; cloudy and drizzly during that time. **Stomach of ASE 2531**: full of part purple, fibrous fruit with hard red seeds; large chunks of a white seed; small pieces of yellowish green mash; pieces of brown material (probably from acorns), a few remains from small adult beetles. **Stomach of ASE 2532**: full, mostly dry and tan acorn mash with chewed remains of a few long-legged cursorial coleopteran larvae, several adult beetles, a scorpion, and a geophilomorph centipede. **Stomach of ASE 2537**: filled with acorn mash, large oblong red seeds (same as in ASE 2531), a small cursorial beetle larva, and abundant remains of adult beetles.
225462 (2536)	1402	Feb. 1974	On slender (2–3 in. diameter) understory tree growing across Sungai Salubeka, about 2 ft above the stream, well downstream in canyon. **Stomach**: full of purple and tan mixture of acorn mash, skin, and large tough seeds of another fruit, chewed remains of several adult beetles, and a grasshopper or katydid (Orthoptera).
223540 (961)	1463	Nov. 1973	In prominent runway on steep slope; caught about 9:00 a.m.
225463 (2459)	1512	Jan. 1974	In prominent damp runway alongside decaying, moss-covered trunk lying on terrace below ridgetop and above deep ravine. Dry oak-chestnut forest (several rotting trunks lying on ground are all chestnuts). **Stomach**: full, mostly acorn mash and remains of arthropods (an ant, an orthopteran, one large adult beetle, a few chewed long-legged cursorial beetle larvae, and a leach).
Sungai Tolewonu 226497 (4061)	168	Jan. 1976	On rotting trunk lying across second large tributary; part of an old tree-fall that is covered with the climbing gingerlike monocot, shrubs, ferns and palm rosettes; about 6 ft above surface of water; caught between 8 and 10:30 a.m. *Rubrisciurus rubriventer*, and the rat, *Maxomys hellwaldii*, were taken on same spot. **Stomach**: half full with mostly figs (chunky pieces of white pulp mixed with tiny amber seeds on stalks); remains of one cursorial coleopteran larva and one adult beetle.
226498 (4073)	290	Jan. 1976	On wet, moss-covered decaying section of trunk that has broken into two pieces and lay in a V across headwater branch of second long tributary. Old and rotten tree-falls are everywhere; many trees had succumbed to old landslides on very steep slopes. Away from these disturbed spots, the steep slopes are covered with intact hill forest; the understory is dense and scrubby; scattered taller trees form a broken canopy. *Pometia pinnata* is common near the stream; tall *Palaquium obovatum* and *Mussaendopsis beccariana* are scattered over the steep slopes and contribute to the top canopy. Squirrel trapped about 7:00 a.m. The rat, *Paruromys dominator*, was taken in same spot. **Stomach:** partially full of a bit of pink and dark gray fruit mash (the gray is remains of figs, endosperm, and tiny seeds) and arthropod remains (an adult beetle, pill bug [Crustacea, Isopoda, Oniscoidea], remains of a large scolopendromorph centipede, a scorpion, and a few ant pupae).

TABLE 51
(Continued)

Locality, AMNH and (ASE) numbers	Elevation (m)	Date	Trap site, other species trapped there, and stomach contents
226499 (4078)	335	Jan. 1976	On moss-covered decaying limb (8 in. diameter, 30 ft long) resting across branch of tributary in headwaters area. Good hillside forest on steep slopes; scattered tall trees form an open, high canopy; understory dense, forming closed canopy; undergrowth thick, especially along banks of ravine, providing good shade; area is cool and wet. Sun ferns, palm rosettes and adults, euphorbs, and figs are common components of understory near streamside. *Pometia pinnata* is common emergent, as is *Pterospermum celebicum*, *Elermerillia ovalis*, and other tall trees. The tree squirrel, *Prosciurillus alstoni*, and rat, *Taeromys celebensis*, were taken at same spot. **Stomach:** distended with semidry pale pinkish purple and tan acorn mash; several large beetle larvae (short, tiny legs, heads bitten off), remains of a scorpion, many pieces of adult beetles (wings, sclerites, legs), and several small ants.

describing samples that represent two species indigenous not to Sulawesi but to forested islands, peninsulae, and mainland in the Indomalayan region west of Sulawesi. Their occurrence on the island represents anthropogenic introductions, likely as pets. We did not survey the skins of these specimens for sucking lice.

THE NONENDEMIC SQUIRRELS REPORTED FROM SULAWESI

Four scientific names associated with Sulawesian squirrels—*microtis*, *erythromelas*, *erythrogenys*, and *schlegelii*—identify two species native to the Sunda Shelf and not part of the endemic Sulawesian sciurid fauna. Here we briefly discuss the identities of each.

Callosciurus notatus (Boddaert, 1785)

Sciurus Notatus Boddaert, 1785: 119.
Sciurus (*Rheithrosciurus*) *microtis* Jentink, 1879: 41.

LECTOTYPE AND TYPE LOCALITY: The lectotype of *Sciurus microtis* is an adult female (RMNH 13349, specimen "*e*" in Jentink's, [1888: 29] catalog) obtained by J.E. Teysmann in 1877. Jentink (1888: 29) incorrectly indicated 1887 to be the year the specimens were collected. Chris Smeenk writes in his unpublished catalog of Leiden mammalian types: "Teysmann worked on Salayar from 16 November to 11 December 1877 (Van Steenis-Kruseman, 1950: 524). The year 1878 given by Jentink (1887, 1888) thus refers to the year when the material was received in Leiden." He explained (in litt., 2008) that " Jentink (or his predecessors, in this case Schlegel) very often confused the years of collection and reception." The lectotype consists of a skin mounted in a live pose and a skull (extracted from the mount after Jentink's tenure at Leiden). The skin is overstuffed, leaving an open seam on the head, and the tail is missing. The skull lacks part of the braincase but is in the best condition and the most complete of all the six syntypes.

Specimen "*e*" was one of six specimens cataloged as types (= syntypes) by Jentink (1888: 29). Following Chris Smeenk's suggestion (in litt., 2008), we select specimen "*e*" as the lectotype, following the rules promulgated in Article 74.1 of the Code (ICZN, 1999: 82). The other five, all collected by J.E. Teysmann in November–December, 1877, become paralectotypes: **(1)** specimen "*a*" (Jentink, 1887: 193, 1888: 29), RMNH 13345, an adult male, skin mounted in live pose and extracted incomplete skull; **(2)** specimen "*b*" (Jentink, 1887: 193, 1888: 29), RMNH 13346, an adult male, skin mounted in live pose and extracted partial skull; **(3)** specimen "*c*" (Jentink, 1887: 193, 1888: 29), RMNH 13347, an adult male, skin mounted in live pose and extracted incomplete skull;

(4) specimen "*d*" (Jentink, 1888: 29), RMNH 13348, an adult female, skin mounted in live pose and extracted incomplete skull; **(5)** specimen "*f*" (Jentink, 1888: 29), RMNH 13350, an adult female, skin mounted in live pose and extracted incomplete skull.

The type locality is Pulau Salayar (06°05′S, 120°30′E) off the southern coast of the southwestern peninsula (see one of the distribution maps for any species of the endemic squirrels), Propinsi Sulawesi Selatan, Indonesia.

REMARKS: In addition to the lectotype and five paralectotypes, we have also examined the six specimens discussed by Sody (1949: 92): MZB 6105–6110.

In his description, Jentink (1879: 41) noted that *microtis* was similar to "*Sciurus nigrovittatus*" (= *Callosciurus nigrovittatus*) in its fur markings, and described the species as follows:

> General colour tawny blackish. On the back the hairs are black with two tawny rings; a few ones are entirely black. On the upperpart of the head and outside of legs, feet and hands the hairs have only one tawny ring. On each side of the body is a tawny lateral streak, consisting of black hairs with long tawny tips. The sides of the body present a darker colour than the upperparts of the back, each hair being here black, with a very minute tawny tip. Chin, throat, chest belly and inside of legs with a beautiful reddish tint, produced by the long reddish tawny coloured tips of the brownish black hairs. Tail shorter than head and body. The hairs are here black with three tawny rings; underparts of the tail near the root and circumference of anus more reddish. A circle around the eyes feeble reddish colored. In-and outside of the very short ears closely covered with short reddish brown hairs. Whiskers and bristles on the cheeks long and black. The well arched claws black with white points. Cutting-teeth orange; upper ones longitudinally grooved.

Major checklists of mammals have identified Jentink's *microtis* as a population of *Callosciurus notatus* occurring on Pulau Salayar (Ellerman, 1940; Laurie and Hill, 1954; Corbet and Hill, 1992; Hoffmann et al., 1993; Thorington and Hoffmann, 2005). The species is of medium body size with dark brown upperparts, buff and black stripes on sides of the body and underparts ranging from gray to chestnut (see measurements and the illustrations in Medway, 1969, and Payne et al., 1985). *Callosciurus notatus* has been documented from peninsular Thailand, the Malay Peninsula; the larger islands of Sumatra, Java, Bali, and Borneo, and some smaller islands on the Sunda Shelf; and Lombok and Salayar to the east of the Shelf (Kitchener et al., 1980; Corbet and Hill, 1992: 291). At least 77 scientific names, originally identifying separate species, or subspecies of *notatus*, have been attached to *C. notatus*, but as Corbet and Hill (1992: 291) noted,

> In spite of the enormous number of named forms, geographical variation is slight compared with that in most other widespread species of *Callosciurus*. The dorsal pelage and tail are very uniform with only a little local darkening, and most variation concerns the colour of the ventral pelage (pale grey to dark chestnut), the clarity of the lateral dark and light stripes, and the extent, or absence, of reddish brown hairs in the tail-tip.

Corbet and Hill wrote of the dull lateral stripes of squirrels in the Salayar sample, and their dull buff venters, which closely resemble some squirrels in samples from Java. The variation in color of underparts of the specimens we examined range from grayish buff to pale orange, and do match samples from Java we studied, as does the intensity of the lateral stripes.

A careful and comprehensive analysis of geographic variation in pelage coloration, morphometric traits, and molecular characteristics for *C. notatus* has yet to be realized. Results of such a study may identifiy discrete populations that represent different species, possibly assemble related geographic populations, and hopefully point to the geographic origin of the populations on Lombok and Salayar. The occurrence of *C. notatus* on those two islands east of the Sunda Shelf may represent natural dispersal, but introduction by humans seems more likely. Chris Smeenk (in litt., 2009) writes us that,

> For ages, there has been an intensive trade, particularly by people from Madura, Celebes (Makassar and the Minahasa) and Ternate, with all parts of the Archipelago. Naturally, Java (e.g., Surabaya) has always been a highly

important and profitable destination. Salayar being at the south end of Celebes and relatively close to Madura and Surabaya, this would have been a very likely place where Javan pets could have landed. The population of Lombok too, must have been introduced, possibly from Bali.

That the species could be an anthropogenic introduction to Salayar is suggested by its habitat and the apparent absence of nearly all endemic Sulawesi mammal species from the island. Today little of the original semi-evergreen rain forest remains on Salayar, and most of the island consists of cleared or cultivated land (see map 8d in MacKinnon, 1997). We have no information about the environment on Salayar where the specimens were collected, but elsewhere within its range *C. notatus* is abundant in gardens, plantations, and secondary forests. On Borneo the squirrel "...can live and breed entirely in monoculture plantations" (Payne et al., 1985: 236). Davis (1962: 78) wrote of Bornean populations: "This species does not appear to be common in the interior of the primary forest, but is abundant around the edges, in clearings, and in secondary growth. It is often seen in towns and cities, and does considerable damage to coconut and rubber plantations." In our experience, the endemic species of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* have been encountered only in primary forest habitats. No sample of any species in those three genera has ever been collected on Pulau Salayar, and of all the species of mammals endemic to Sulawesi, only a tarsier has been recorded from the island (Groves, 2005: 128).

Although the origin of the Salayar population is unresolved, we do know that *C. notatus* is a member of the Sundaic mammalian fauna, that it has never been recorded from the mainland of Sulawesi or any other offshore island than Pulau Salayar, and that it is phylogenetically not closely related to the endemic Sulawesian species of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*.

Callosciurus prevostii (Desmarest, 1822)

Sciurus erythromelas Temminck, 1853: 248.

Sciurus erythrogenys Schlegel, 1863: 29, pl. 2, fig. 3; not Waterhouse (1942 [1943]).

Sciurus Schlegelii Gray, 1867: 278 (= *Macroxus Schlegelii* Gray, 1867: 278).

The three scientific names are attached to two specimens that differ conspicuously in coloration of fur, but likely represent the same species: *Callosciurus prevostii*. We explain our reasons for this allocation in the following paragraphs.

The lectotype of *Sciurus erythromelas* is an adult male (RMNH 13378, specimen "*bb*" in Jentink's [1888: 27] catalog) obtained by E.A. Forsten sometime betwen 1840 and 1842. The lectotype consists of a skin mounted in a live pose and a skull (extracted from the mount after Jentink's tenure at Leiden). The skin is in very good condition except for slight damage to the mouth caused when the skull was extracted. The occiput, one ectotympanic bulla, and one zygomatic arch are missing from an otherwise complete skull. Specimen "*bb*" was one of two specimens cataloged as types (= syntypes) by Jentink (1888: 27). Following Chris Smeenk's suggestion ("It is perfect for a lectotype," in litt., 2009), we select specimen "*bb*" as the lectotype, following the rules promulgated in Article 74.1 of the Code (ICZN, 1999: 82). The type locality is Kema (01°22′N, 125°03′E; locality 8 in gazetteer for *Prosciurillus leucomus* and map in fig. 11), near sea level on the coastal plain of the northeastern end of the northern peninsula, Propinsi Sulawesi Utara, Indonesia. RMNH 13378 is also the holotype of *Sciurus erythrogenys* Schlegel, 1863 and *Macroxus schlegelii* Gray, 1867 (see the discussion to follow).

The other specimen, also collected by E.A. Forsten between 1840 and 1842, but from Manado (01°30′N, 124°50′E; locality 4 in gazetteer for *Prosciurillus leucomus* and map in fig. 11) on the coastal plain near sea level, is the paralectotype of *Sciurus erythromelas*: specimen"*cc*" (Jentink, 1888: 27), RMNH 13379, an adult male. The skin, mounted in a live pose with the skull still in the skin, is in good condition, and retains its bright color pattern.

Chris Smeenk is preparing a catalog of the "Type-specimens of recent mammals in the National Museum of Natural History, Leiden" and gave us permission to quote his account for *Sciurus erythromelas*, which is the best place to begin our discussion of the type specimens. Chris writes that:

Temminck (1853) does not state how many specimens he had before him; he writes: "Il est heureux que nous ayons pu recevoir cet écureuil nouveau dans son pelage des noces ou à l'époque du rut, en même temps que nous sont parvenus, de la même contrée, des individus tués dans la saison opposée de l'année; obtenus séparément et capturés dans des localités différentes," so one may conclude that he had more than two skins ["Reading the French text carefully, one must conclude that he had several specimens before him of different coloration and from various localities, but only two are left, both collected by Forsten"; C. Smeenk, in litt., 2009]. The provenance is specified (p. 249) as "Les patries septentrionales de Célèbes, Gorontalo et Kema." There are now two specimens in the Leiden Museum, from Manado and Kema, none from Gorontalo; no collection date is recorded, so it is not clear why Temminck concluded that the differences in coloration were seasonal. The animal from Manado (RMNH 13379) is also described and illustrated by Schlegel (1863: 28–29, pl. 2 fig. 2), who redescribes the specimen from Kema (RMNH 13378) as *Sciurus erythrogenys*. ...

Forsten collected in NE Celebes between March 1840 and April 1842. ... His diary, a copy of which (in an unknown hand) is preserved in the archives of the Leiden Museum, sheds no light on the exact provenance and collection dates of these animals. The squirrels described here must have been introduced from Borneo (Musser, 1987: 80), perhaps as pets; the coastal towns of Manado, Kema and Gorontalo have always been centres of trade.

Ten years after Temminck's account was published (see appendix 6 for Temminck's description in the original French), Schlegel's [1863: 29] description of *Sciurus erythrogenys* appeared. Schlegel regarded the squirrels from NE Celebes described by Temminck (1853: 248) as *Sciurus erythromelas* to represent two distinct species. He restricted the name *S. erythromelas* to the specimen from Manado (RMNH 13379) and described the squirrel collected at Kema (RMNH 13378) as *S. erythrogenys*, named for its reddish cheeks (the description in the original French is provided in appendix 7).

Gray (1867: 278) later renamed the same specimen: "*Sc. schlegelii* (with cheeks red), *Sc. erythrogenys*, Schlegel, *l. c.* t. 2. f. 3 (1863), not Waterhouse" because *erythrogenys* was proposed earlier by Waterhouse (1842 [1843]) for the African red-cheeked rope squirrel *Funisciurus leucogenys* (Waterhouse, 1842). As Thorington and Hoffmann (2005: 792) explained, "Waterhouse (1842 [1843]) renamed this species [*F. leucogenys*] *erythrogenys*, 'red-cheeked' in an attempt to replace the inappropriate name *leucogenys*, 'white-cheeked.' This is an unjustified emendation."

Gray proposed *schlegelii* within his account of *Macroxus atrocapillus* (= *Sciurus atricapillus* Schlegel, 1863; incorrectly quoted by Gray as "*atrocapilla*"; *atrocapillus* is currently treated as either a synonym of *Callosciurus prevostii* or a valid subspecies, *C. p. atrocapillus*; Payne et al., 1985; Corbet and Hill, 1992; Thorington and Hoffmann, 2005). Gray's wording, "*Sc. Schlegelii* (with cheeks red), *Sc. erythrogenys*, Schlegel, *l. c.* t. 2. f. 3 (1863), not Waterhouse," was meant to explicitly identify *schlegelii* as a replacement name for Schlegel's *erythrogenys* within *Sciurus*, the genus in which Schlegel described *erythrogenys*. Gray used *Macroxus* for species of Oriental squirrels, not *Sciurus*, so the correct combination for his replacement name is *Macroxus schlegelii* (we are grateful to Chris Smeenk and Al Gardner for their insight into this nomenclatural issue).

RMNH 13378 is the holotype of both *Sciurus erythrogenys* Schlegel, 1863, and *Macroxus schlegelii* Gray, 1867, as well as the lectotype of *Sciurus erythromelas* Temminck, 1853 (see above).

The two specimens are differently colored. The upperparts of the head and body as well as the tail of the lectotype of *Sciurus erythromelas* (RMNH 13378 from Kema) is dark brown speckled with buff and black, including the outside of the limbs. Sides of the body are marked by a whitish gray stripe above a black stripe. The underparts are reddish orange, which extends to the inside of the front and hind limb but not to the feet, which are black, and the cheeks and throat are orange-red.

The paralectotype of *Sciurus erythromelas* (RMNH 13379 from Manado) is appreciably darker. The head and back, back of the thighs, and tail are blackish. A single pale stripe (brownish black speckled with gray) marks each side of the body (no black stripe). The area around the mouth, cheeks, shoulder, upper arms, and front of the thighs are

brownish black speckled with buff (appears grizzled). The underparts from chin to base of the tail, including most of the forearms (the blackish upperparts extend along the outside of the forearms as a narrow blackish stripe towards the front feet) are dark reddish orange; sides of the feet and parts of the dorsal surfaces are the same color (although tops of the hind feet are washed with brownish black).

To us, the color patterns of the two types are reminiscent of *Callosciurus prevostii*, a Sundaic endemic occurring on peninsular Thailand and Malaya, the larger Sundaic islands of Sumatra and Borneo, and smaller islands on the Sunda Shelf, but not Java (Corbet and Hill, 1992; Thorington and Hoffmann, 2005). The species is medium in body size (length of head and body, 200–267 mm; length of tail, 202–273 mm; length of hind foot, 45–61 mm; weight, 250–500 g; see Medway, 1969; Payne et al., 1985), physically smaller than the Sulawesian *Rubrisciurus rubriventer*, but larger than species in the *Prosciurillus leucomus* group (see table 3). On Borneo, tall and secondary forests are the habitat of *C. prevostii*, where it stays mostly in the upper canopy, descending to the ground when necessary to cross gaps in the canopy; it will also enter gardens and plantations next to tall forest (Davis, 1962; Payne et al., 1985: 234). In parts of the Malay Peninsula, the squirrel is locally common in oil plantations and adjacent forest, and is "popular as a pet because of its bright coloration" (Medway, 1969: 59).

Probably no other species of *Callosciurus* is as geographically variable in color patterns of the fur, not only among peninsular and insular landmasses but also within large islands, especially so among populations on Borneo (Corbet and Hill, 1992; Musser's study of specimens representing Indomalayan species). Payne et al. (1985; pl. 24) provide color renditions of the primary chromatic patterns found among Bornean populations and their general distribution on the island. Some populations exhibit intergradation in these patterns, other populations isolated by rivers apparently do not.

In his list of squirrel specimens in Leiden, and his catalog of mammals in that institution, Jentink (1883: 132, 1888: 27, respectively) listed the types of *erythromelas* and *erythrogenys* (including *schlegelii*) under "*Sciurus prevostii*." Later checklists arranged *erythromelas* and *schlegelii* each as a subspecies of *Callosciurus prevostii* with both occurring on Sulawesi (Ellerman, 1940: 367; Laurie and Hill, 1954: 92) or associated with Bornean *C. prevostii* but unassigned as to subspecies status (Hoffmann et al., 1993: 423; Thorington and Hoffmann, 2005: 279); none of these checklists published after Jentink's catalog listed Schlegel's *erythrogenys*.

We agree with Jentink's (1888: 27) identification of the lectotype and paralectotype of *erythromelas* as examples of *Callosciurus prevostii*. The population of *C. prevostii* living in northern Borneo in Sabah and northeastern Sarawak, *C. p. pluto*, is black with bright reddish orange underparts, and some specimens show a weak whitish body stripe (see Payne et al., 1985, pl. 24); the coloration closely resembles the paralectotype of *Sciurus erythromelas* (RMNH 13379) from Manado; the minor differences could easily be ascribed to individual variation.

The brighter lectotype of *Sciurus erythromelas* could be a color variant of Bornean *C. prevostii*. It does not exactly match any of the color examples illustrated by Payne et al. (1985, pl. 24), but its color pattern does fall somewhere between that illustrated for *C. p. atricapillus* from eastern Sarawak (possessing dark hind feet and limbs) and that for *C. p. caroli* from farther to the northeast in Sarawak (with orange-red throat and cheeks). Corbet and Hill (1992: 290–291) listed *S. erythromelas* (along with *S. schlegelii*) as a synonym, with question, of *Callosciurus baluensis*, an endemic of the north Bornean mountains in Sabah and Sarawak, with an altitudinal range of 300 to 2000 m: "The type of *erythromelas* (Leiden Museum) matches Bornean *C. baluensis* rather closely in pelage but has more orange-brown on the cheeks." Musser examined the holotype of *baluensis*, and other specimens, including the holotype of *baramensis*, the other name associated with *C. baluensis*. None of the examples of *C. baluensis* has the orange-red cheeks and black feet seen in the lectotype of *Sciurus erythromelas*.

For now we prefer to associate *erythromelas* (along with *erythrogenys* and *schlegelii*)

with Bornean *C. prevostii* rather than *C. baluensis*. This identity can be tested in two ways. Although the skull of the lectotype of *erythromelas* is damaged, enough of its dimensions could be measured and the values compared with those obtained from samples of *C. baluensis* and geographic samples of *C. prevostii* from Borneo in a multivariate analysis (principal-components analysis, for example). Results from analyses of DNA sequences extracted from hairs or bits of dry skin from the lectotype of *erythromelas* and samples of *C. baluensis* and *C. prevostii* would also be revealing. If in the future, the lectotype of *Sciurus erythromelas* can be unambiguously identified as an example of *C. baluensis*, that latter name will have to be changed to *Callosciurus erythromelas*, which would then be a species with its indigenous range in northern Borneo, but its type locality outside of that range in northeastern Sulawesi.

We do not know how many specimens (and their collection localities) Temminck (1853) originally used for his description of *Sciurus erythromelas*. We do know that two remain in the collection at Leiden, that each is different in color pattern, that no other specimen resembling either one has ever been collected on Sulawesi since Forsten's activities between 1840 and 1842, and that the two types do not represent any species of squirrel truly endemic to Sulawesi. Both specimens are likely examples of geographic variation described for the populations of *Callosciurus prevostii* on Borneo. We suspect the material obtained by Forsten to have originally been transported as pets from Borneo to the Minahasa region (in which the coastal towns of Kema and Manado are located).

With this last account, we leave the squirrels and turn to the eight species of sucking lice parasitizing eight of the 10 species of Sulawesi's endemic squirrels. All samples of lice represent new species, and their descriptions are contained in the following segment of our report.

THE SPECIES OF SUCKING LICE FROM THE SQUIRREL HOSTS

Seven subheadings contain information covering descriptions of each of the eight new species of sucking lice, all of which belong to the genus *Hoplopleura* (Hoplopleuridae): **(1)** holotype of the species of *Hoplopleura* and type locality of the squirrel host; **(2)** referred specimens of lice to a new species; **(3)** geographic distribution on Sulawesi; **(4)** etymology; **(5)** diagnosis; **(6)** description; **(7)** relevant remarks. Refer to the preceding sections for classification of the squirrel hosts as well as morphological characteristics of each host species, its geographic and altitudinal distributions on Sulawesi, its ecology, and other information.

Hoplopleura rubrisciuri, new species

HOLOTYPE AND TYPE LOCALITY: Male and allotype female *ex* male *Rubrisciurus rubriventer* (AMNH 225491; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by G.G. Musser at 4960 ft (1512 m) on Gunung Kanino (1°17′S, 120°08′E; see gazetteer and fig. 5), Propinsi Sulawesi Tengah, Indonesia, on 31 January 1975. The holotype is deposited in USNM.

REFERRED SPECIMENS: An additional 5 males, 11 females, and 4 nymphs from the same pelt as the holotype and allotype; two nymphs *ex* male *R. rubriventer* (AMNH 224052) collected by G.G. Musser at 675 m at Sungai Sadaunta (1°23′S, 119°58′E), central Sulawesi on 9 February, 1974; one female *ex* female *R. rubriventer* (identified in the field by L.A. Durden and I.A. Hanski) collected by I.A. Hanski at ca. 1100 m on Gunung Maujat (0°45′N, 124°25′E), on the northern peninsula of Sulawesi (Sulawesi Utara), on 5 February, 1985; one male *ex* female *R. rubriventer* (BM 40.674) collected by W.J.C. Frost at 4000 ft (1220 m) in the Luartes Range, Pegunungan Quarles, Bulu [= Gunung] Karua (referred to as "Rantekaroa, Quarles Mt." on specimen tags), 02°56′S, 119°39′E), central Sulawesi, on 13 December, 1939; one male *ex* female *R. rubriventer* (AMNH 101316) collected by G. Heinrich at 50 m at Wawo (3°41′S, 121°02′E), on the southeastern peninsula of Sulawesi, on 23 January, 1932. Paratypes are deposited in AMNH, BMNH, LAD, and USNM.

DISTRIBUTION: Known only from the five collections listed above, all from *Rubrisciurus*

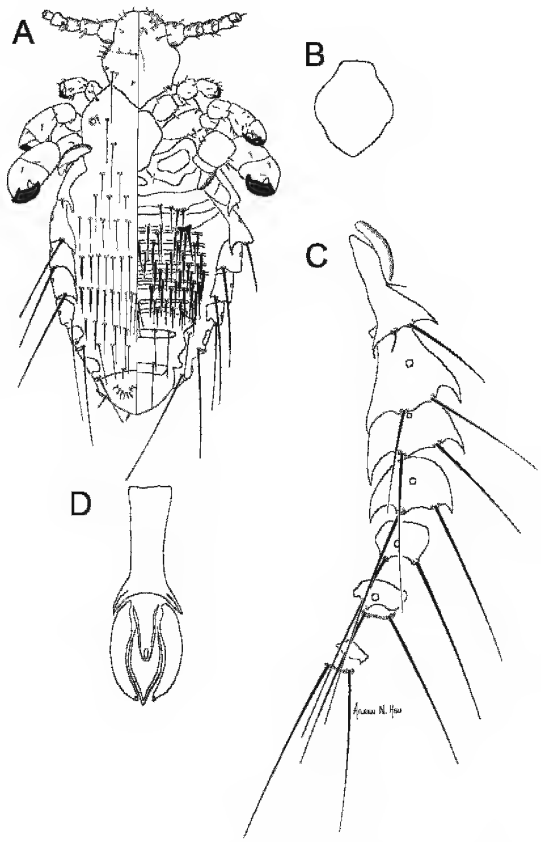

Fig. 46. *Hoplopleura rubrisciuri*, male. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

rubriventer. *Hoplopleura rubrisciuri* probably parasitizes *R. rubriventer* throughout its geographic and altitudinal ranges (see fig. 11 and table 4).

ETYMOLOGY: This louse is named for the monotypic host genus.

DIAGNOSIS: *Hoplopleura rubrisciuri* is a distinctive louse. It can be distinguished from all other species of *Hoplopleura* using a combination of the following characters: **(1)** the absence of dorsal abdominal plates in both sexes and the absence of sternal abdominal plates (between the 3rd sternal plate and the subgenital plate), in the female, N.B., a wrinkled texture is characteristic of the abdomen in some specimens that superficially gives the impression of numerous narrow plates; **(2)** the presence of one short and one long apical seta on paratergal plate II and of two long apical setae on each of paratergal plates III–VIII in both sexes; **(3)** the shape and proportions of the thoracic sternal plate and of the genitalic structures in both sexes.

DESCRIPTION: Abbreviations used here and in descriptions of the other species of lice to follow are explained in Specimens and Methods.

Male (fig. 46A–D). Length of holotype 1.02 mm (mean for series 1.01, range 0.92–1.08, $N = 8$). Head and thorax well sclerotized.

Head. Slightly longer than wide with broadly rounded anterior apex; 3 SuHS, 4 DMHS, 1 DPoCHS, 1 SpAtHS, 2 ApHS (1 dorsal, 1 ventral), 4 AnMHS (2 dorsal, 2 ventral), 2–3 VPaHS, and 1 VPHS on each side; DPHS fairly long, extending to thoracic spiracle, with 1 DAcHS medial to DPHS. *Antenna.* 5-segmented with basal segment much larger than second segment, slightly wider than long.

Thorax. About as broad as long; thoracic sternal plate (fig. 46B) blunt anteriorly and tapering to broad apex posteriorly; mesothoracic spiracle moderate in size (0.020 mm in diameter) with one small DMsS and one fairly long DPTS (0.14 mm in length) medial to spiracle. *Legs.* Forelegs small, each with narrow acuminate claw; hind coxa and claw robust; midlegs intermediate in size between fore and hindlegs.

Abdomen. Wider than thorax; no dorsal plates; two plates per segment ventrally on segments 2–6; first ventral plate small, plates 2 and 3 broad, well sclerotized, and extending laterally to articulate with corresponding paratergal plates; ventral plate 3 with two robust lateral setae on each side (three on one side in one specimen); ventral plates 4–12 narrow and poorly sclerotized; one row of DCAS per segment dorsally, first row with 2 DCAS, 2nd row with 4 DCAS, rows 3 and 8 each with 6 DCAS, rows 4–7 each with 10–17 DCAS; most DCAS long and thin except for a few dagger-shaped lateral setae; 11 rows of 7–10 StAS ventrally; 1 VLAS lateral to each of ventral plates 8–11 on each side. *Paratergal plates* (fig. 46C) present on segments 1–8: plate I lacking setae; plate II with one long and one short apical seta; plates III–VIII each with two long apical setae; plates II–V subtriangular and with both apices

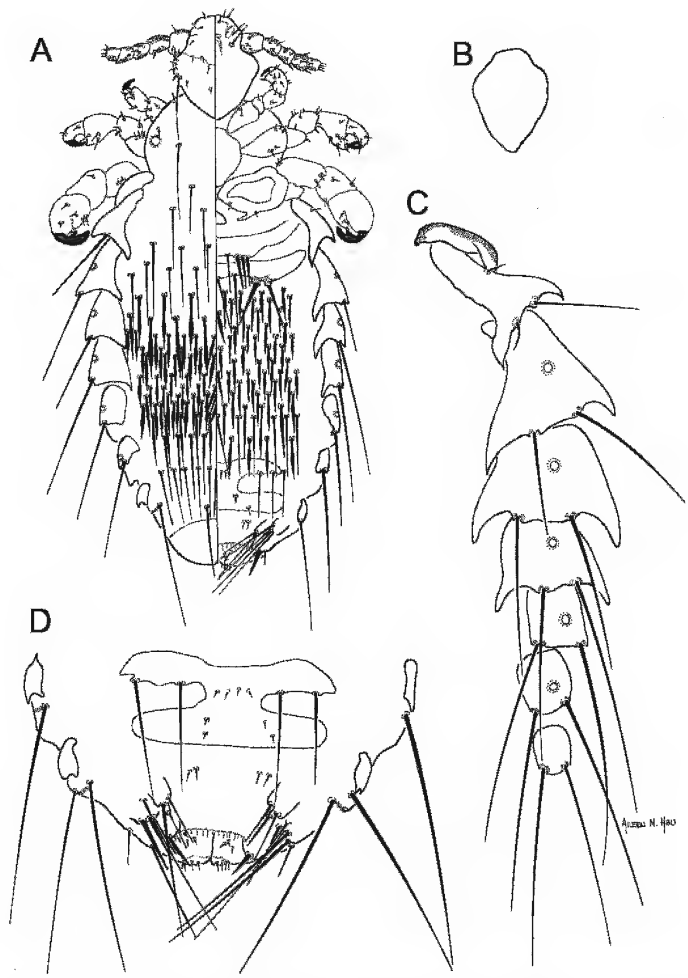

Fig. 47. *Hoplopleura rubrisciuri*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

developed into points; plates III–VII each with moderate-size spiracle.

Genitalia (fig. 46D). Long subgenital plate (extending anteriorly to level of paratergal plate VI in most specimens) with characteristic undulating lateral margins (as shown in fig. 46A); aedeagal basal apodeme slightly longer than parameres; parameres broad, curved, and tapering apically; pseudopenis short, barely extending beyond apices of parameres.

Female (fig. 47A–D). Length of allotype 1.31 mm (mean for series 1.18, range 0.92–1.33, $N = 13$).

Head, thorax, and legs. As in male unless indicated otherwise. 1 DAnCHS and 2 SpAtHS on each side of head. Thoracic sternal plate (fig. 47B) similar to that of male but slightly broader.

Abdomen. Wider than thorax; lacking dorsal plates; ventrally with only three anterior plates (plate 1 small, plates 2 and 3 both broad and articulating with corresponding paratergal plates) and subgenital plate; 16–17 rows of DCAS, first and last rows each with two setae, row 2 with four setae, rows 3–6 each with 6–8 setae, and rows 9–15/16 each with 8–13 setae; DCAS in rows 1–4 and in posterior three rows long and narrow; most DCAS in rows 5–13/14 dagger-shaped; 7–8 StAS on ventral plates 2–3; two robust lateral setae on each side on plate 3; 13–14 rows of

VCAS posterior to plate 3 each with 7–11 setae; most VCAS dagger-shaped. *Paratergal plates* (fig. 47C) as in male except for minor differences in shapes of plates as illustated.

Genitalia (fig. 47D). Subgenital plate with deep lateral indentation on each side and four long setae (two on each side) on anterior arms of plate; eight small setae on subgenital plate (four central and two situated proximally on each posterior arm); gonopod VIII with three apical setae of moderate length; gonopod IX with one short stout seta; vulvar fimbriae present.

REMARKS: *Hoplopleura* sp. D listed by Durden (1986) is *Hoplopleura rubrisciuri*.

Hoplopleura leucomus, new species

HOLOTYPE AND TYPE LOCALITY: Female *ex* male *Prosciurillus leucomus* (USNM 218077; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by H.C. Raven at 200 m at Labuan Sore (00°37′S, 120°03′E; see gazetteer and fig. 11), Propensi Sulawesi Tengah, Indonesia on 1 December, 1916. The holotype is deposited in the USNM.

REFERRED SPECIMENS: In addition to the holotype female, two more female specimens, one from the same host (USNM 218077) as the holotype, the other *ex* male *Prosciurillus leucomus* (AMNH 196566) collected by G. Heinrich at 900 m at Rurukan (01°21′N, 124°52′E; see gazetteer and fig. 11), Propensi Sulawesi Utara, Indonesia on 22 January 1931.

DISTRIBUTION: *Hoplopleura leucomus* is known only from *Prosciurillus leucomus*, which is recorded from voucher hosts collected at 200 and 900 m. This tree squirrel occurs throughout lowland and montane altitudes in the northern peninsula of Sulawesi and on Pulau Lembeh off the northeastern coast (see fig. 11 and table 4).

ETYMOLOGY: Named for the specific epithet of the host species.

DIAGNOSIS: Females of *Hoplopleura leucomus* can be distinguished from females of all other species of *Hoplopleura* using a combination of the following characters of the female genitalia and associated structures, which are all shown in figure 48E: **(1)** the distinct shape of the subgenital plate which appears as two laterally elongate plates that are connected medially; **(2)** the presence of two long setae laterally on each side of the upper section of the subgenital plate together with four central setae (two lateral setae of medium size, two small central setae) in the anterior portion of the lower section of the subgenital plate; **(3)** the elongate shape and setation (especially the more recessed insertion of the middle of the three setae) of the gonopods VIII. Females of *Hoplopleura leucomus* have morphological similarities to females of the other species of *Hoplopleura* described from Sulawesi squirrels in this report in that the subgenital plates all show tendencies toward being separated into two major sections, one anterior and one posterior. In some species, the plate sections are joined medially whereas in others the plates are completely separated. This subgenital plate conformation is rare in females of other species of *Hoplopleura* regardless of their host(s) or geographic distribution. Although females of all eight of the species of *Hoplopleura* we describe from Sulawesi squirrels in this report show this morphological trend, a glance at the plates of the females for each of the eight species will immediately show that the species are all very easily separated using only the distinctive morphology and setation of this structure.

DESCRIPTION: **Female** (fig. 48A–E). Length of holotype 1.22 mm (mean for series 1.30; range 1.21–1.47, $N = 3$). Head, thorax, and abdomen well sclerotized.

Head. Longer than wide with broadly rounded anterior apex; 2 SuHS, 4 DMHS, 1 DAnCHS, 1 SpAtHS, 3–4 AnMHS, and 1 VPHS on each side; DPHS fairly long, extending to mesothoracic spiracle, with 1 DAcHS medial to DPHS on each side. *Antennae.* 5-segmented with basal segment much wider than second segment, wider than long; second segment elongate.

Thorax. Slightly broader than long; thoracic sternal plate (fig. 48B) with broadly rounded anterior apex, tapering, broadly rounded posterior apex, and broadly rounded lateral margins; mesothoracic spiracle moderate in size (0.019 mm in diameter); DPTS moderate in length (0.12 mm) almost extending to mid region of level of paratergal plate I; no DMsS evident. *Legs.* Fore and

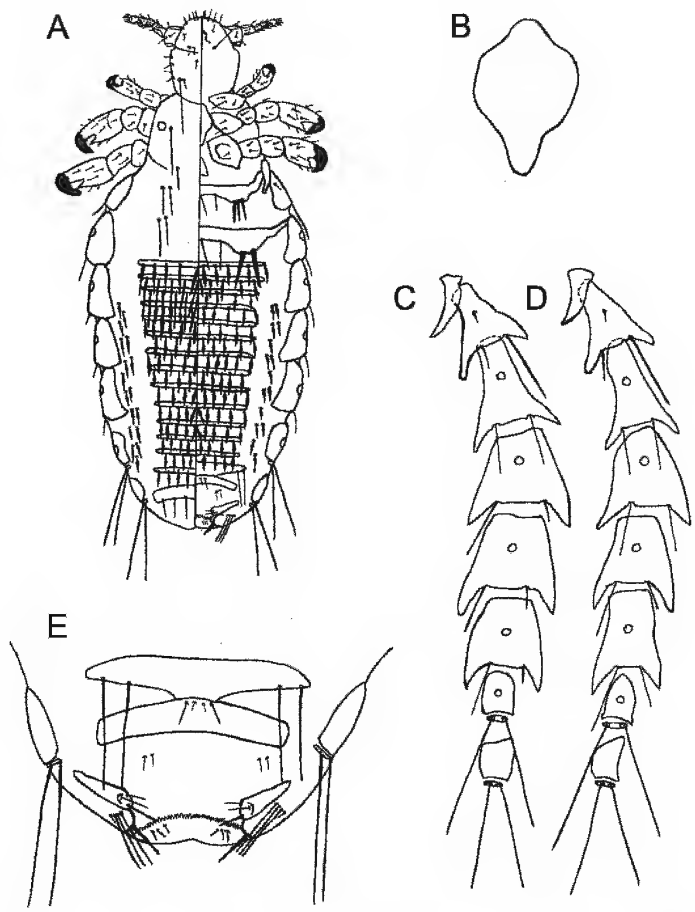

Fig. 48. *Hoplopleura leucomus*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C, D,** paratergal plates showing slight variation between specimens from two geographic regions (C is from the holotype louse from Labuan Sore in Central Sulawesi, D is from a louse specimen from Rurukan in north Sulawesi); **E,** genitalia.

mid coxae subtriangular; forelegs small each with narrow acuminate claw; hindlegs robust each with broad acuminate claw; midlegs intermediate in size between fore and hind legs.

Abdomen. Wider than thorax; 15 plates dorsally comprising three narrow plates on each of segments 4–7, two narrow plates on segment 8 and one broad, curved plate posteriorly; no dorsal plates on segments 1–3; one broad plate per segment ventrally on each of segments 2 and 3; three narrow plates per segment ventrally on each of segments 4–7, and one narrow plate on segment 8; first row of DCAS with two long, thin setae, second and third rows each with four long, thin DCAS, followed by three rows of long, slightly stouter TeAS each with 8–10 TeAS and then by 11 rows of 8–10 dagger-shaped TeAS, and one row of six long, thin TeAS; 10 rows of 1–2 DLAS on each side between segments 4–8; first ventral plate without setae; other ventral plates anterior to subgenital plate each with 8–10 StAS; ventral plates 2 and 3 each articulating with corresponding paratergal plates; ventral plate 2 with three stout lateral StAS on one side (as shown in fig. 48A; two on the other side) and three narrow medial StAS; ventral plate 3 with two robust lateral StAS on each side and three narrow medial StAS; ventral plates 4–16 all with dagger-shaped StAS. *Paratergal*

plates (fig. 48C, D, showing variation) present on segments 1–8: plate II with one long apical seta and one of intermediate length; plate III with two apical setae of intermediate length; plates IV–VI each with one apical seta of intermediate length and the other shorter in length (especially in specimens from Labuan Sore in central Sulawesi as shown in fig. 48C); plates VII and VIII each with two long apical setae; plates I–VI subtriangular; plates II–VI each with both apical angles produced into points; plates III–VII each with moderate size spiracle.

Genitalia (fig. 48E). Subgenital plate with deep lateral indentation on each side and appearance of two separate plates joined medially; two long lateral setae on each anterior arm of subgenital plate; one seta of intermediate length on each side on posterior demarcation of area where two plates appear to be joined, and two small medial setae; gonopods VIII with three apical setae with the middle of these three setae being recessed laterally from plate margin and posterior seta slightly larger than other two setae; gonopod IX with one stout seta; vulvar fimbriae distinct.

REMARKS: Often, male genitalia have important distinguishing characters that delineate different species of congeneric sucking lice. Unfortunately, no males of *H. leucomus* were available for study. Nevertheless, we decided to describe this species based only on female specimens for two reasons. First, as discussed above, the subgenital plate and its associated setae are highly distinctive for this new species as is the subgenital plate morphology for each of the squirrel-associated lice we describe in this report. Secondly, *Hoplopleura leucomus* likely cospeciated with its host, *Prosciurillus leucomus*; that host along with each of the other seven Sulawesi squirrel species from which we obtained lice has a unique species of louse. The slight differences we note between the lengths of apical setae on some of the paratergal plates (see fig. 48C, D) on lice collected from *Prosciurillus leucomus* from different geographic regions are minor and reflect variation within the limits of a single species. The distinctive female genitalic structures, especially of the subgenital plate and its associated setae, are taxonomically more important and are the same in all three specimens we examined regardless of geographic origin. Obviously, it will be important to collect and describe the male of this species and to compare the morphology of lice from *P. leucomus* from different localities if more specimens become available. Molecular analyses using fresh louse samples would also be desirable.

Hoplopleura alstoni, new species

HOLOTYPE AND TYPE LOCALITY: Female *ex* female *Prosciurillus alstoni* (USNM 219519; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by H.C. Raven at 31 m at Pinedapa (01°25′S, 120°35′E; see gazetteer and fig. 11), Propensi Sulawesi Tengah, Indonesia on 15 February, 1918. The holotype is deposited in the USNM.

REFERRED SPECIMENS: The holotype is the only example of the species.

DISTRIBUTION: *Hoplopleura alstoni* is known only from *Prosciurillus alstoni*, which is recorded from a voucher host collected at 31 m. The tree squirrel is found at lowland elevations in the northeastern portion of the central core of Sulawesi, its east-central arm, and the southeastern peninsula and offshore islands (see fig. 11 and table 4).

ETYMOLOGY: Named for the specific epithet of the host species.

DIAGNOSIS: The female of *Hoplopleura alstoni* can be distinguished from females of all other species of *Hoplopleura* using a combination of the following characters: **(1)** the shape and length of the apical paratergal setae; **(2)** the almost flat anterior apex of the head; **(3)** the distinctive shape, proportions, and setation of the genitalia (fig. 49D), especially the shape of the subgenital plate and the positions and lengths of its associated setae. Females of all eight of the species of *Hoplopleura* described from Sulawesi squirrels in this report are easily distinguished from each other (and from all other species of *Hoplopleura*) by the distinctive shapes of their subgenital plates and the characteristics (positions and lengths) of the setae attached to these plates.

DESCRIPTION: **Female** (fig. 49A–D). Length of holotype 1.43 mm. Head, thorax, and abdomen well sclerotized.

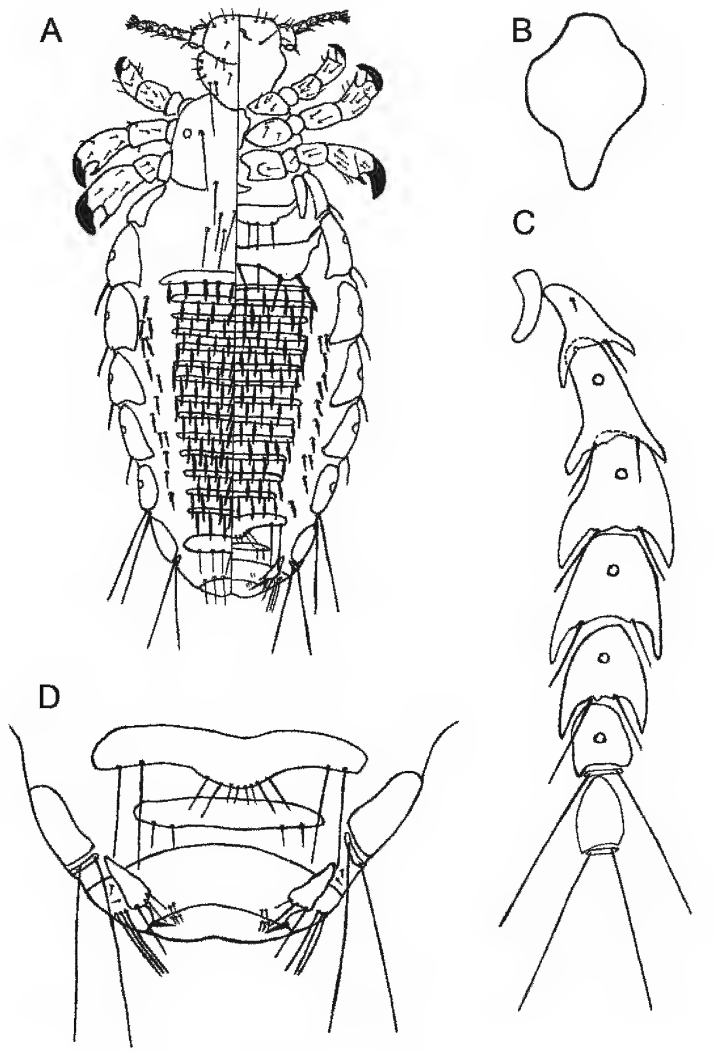

Fig. 49. *Hoplopleura alstoni*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

Head. Longer than wide with blunt, almost flat, anterior apex; 2 SuHS, 3 DMHS, 1 DAnCHS, 3 AnMHS, and 1 VPHS on each side; DPHS fairly long, extending to mesothoracic spiracle, with 1 DAcHS medial to DPHS. *Antennae.* 5-segmented with basal segment much wider than second segment, wider than long; second segment elongate.

Thorax. Slightly broader than long; thoracic sternal plate (fig. 49B) with broadly rounded anterior apex, tapering, fairly broadly rounded posterior apex and broadly rounded lateral margins; mesothoracic spiracle moderate in size (0.021 mm in diameter); DPTS fairly long (0.16 mm), extending to mid-region of paratergal plate II; no DMsS evident. *Legs.* Fore and mid coxae subtriangular; forelegs small each with narrow acuminate claw; hindlegs robust each with broad acuminate claw; midlegs intermediate in size between fore and hind legs.

Abdomen. Wider than thorax; 15 plates dorsally with three narrow plates on each of segments 4–7, two narrow plates on segment 8, and one broad plate on segment 9; 16 plates ventrally anterior to subgenital plate with one small plate on segment 1, one broad plate on each of segments 2 and 3, three

narrow plates on each of segments 4–7, and one narrow plate on segment 8; first and second rows of DCAS each with two long narrow setae, third row with four long narrow DCAS, followed by 14 rows of TeAS each with 6–9 dagger-shaped setae and then by one row of six narrow TeAS; 11 rows of 1–2 DLAS on each on each side extending from segments 4–8; first ventral plate without setae; ventral plates 2–16 each with 6–10 StAS; ventral plate 2 with six long, narrow StAS; ventral plate 3 with two robust StAS on each side and three narrow medial StAS; ventral plates 4–16 each with dagger-shaped StAS; plates 2 and 3 each articulating with corresponding paratergal plates. *Paratergal plates* (fig. 49C) present on segments 1–8: plate II with one apical seta of intermediate length but with other apical seta broken at base (on both sides); plates III–VI each with two apical setae of intermediate length but with one seta slightly longer than other seta on each plate; plates VII and VIII each with two long apical setae; all plates subtriangular; plates II–VI each with both apical angles produced into points; plates III–VII each with moderate size spiracle.

Genitalia (fig. 49D). Subgenital plate separated into two laterally elongate, broad sections with anterior plate distinctly larger than posterior plate; anterior section of subgenital plate curved with posterior, medial, broadly rounded apex bearing eight setae consisting of two setae of intermediate length on each side and four small medial setae; two long lateral setae also present on each side of anterior section of subgenital plate; posterior section of subgenital plate subeliptical and with two fairly small lateral setae on each side; gonopods VIII each with three apical setae increasing in length from anterior to posterior; gonopods IX each with one stout seta; vulvar fimbriae indistinct.

Remarks: Because only the holotype female was available for this new species, many of the remarks made above for *Hoplopleura leucomus*, for which only three females were available, could be repeated here. We decided to describe *H. alstoni* based only on the holotype female because the subgenital plate and its associated setae are highly distinctive and because this louse evidently cospeciated with its host. The result of this apparent cospeciation is that each of the eight Sulawesi squirrel species from which we obtained lice has a unique species of louse. Obviously, the male of *Hoplopleura alstoni* should be described if additional material becomes available.

Hoplopleura topapuensis, new species

Holotype and Type Locality: Male *ex* male *Prosciurillus topapuensis* (USNM 219493; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by H.C. Raven at 1800 m at Rano Rano (1°30′S, 120°28′E; see gazetteer and fig. 11), Propensi Sulawesi Tengah, Indonesia on 21 December, 1917. The holotype is deposited in USNM.

Referred Specimens: One additional male, 12 females (including allotype), 1 nymph *ex* male *P. topapuensis* (AMNH 225505) collected by G.G. Musser at 4900 ft (1509 m) on Gunung Kanino (01°17′S, 120°08′E) on 11 May, 1975; 2 females *ex* male *P. topapuensis* (AMNH 226932) collected by G.G. Musser at 1000 m at Tomado, Danau Lindu (1°19′S, 120°03′E) on 15 August, 1973; 2 females *ex* male *P. topapuensis* (AMNH 223532) collected by G.G. Musser at 4800 ft (1463 m) on Gunung Kanino (1°17′S, 120°08′E) in November 1973. All localities are in the central core of Sulawesi (Propinsi Sulawesi Tengah). Paratypes are deposited in AMNH, BMNH, LAD, and USNM.

Distribution: *Hoplopleura topapuensis* is known only from *Prosciurillus topapuensis*, which is restricted to middle elevations and mountains in the central core of Sulawesi (see fig. 11 and table 4). It has been collected from squirrels trapped at elevations between 1000 m and 1463 m.

Etymology: *Hoplopleura topapuensis* has been named for the specific epithet of its host.

Diagnosis: *Hoplopleura topapuensis* can be distinguished from all other species of *Hoplopleura* using a combination of the following characters: **(1)** the presence of three dorsal abdominal plates posteriorly in the male; **(2)** the shape of the thoracic sternal plate; **(3)** the shape and length of the apical paratergal setae in both sexes; **(4)** the shape,

proportions, and setation of the male and female genitalia. This species is morphologically similar to *Hoplopleura murinus* n. sp., a parasite of *Prosciurillus murinus*, which is also described in this paper. These two species of *Hoplopleura* can be distinguished using the following characters. Males: **(1)** five dorsal abdominal plates posteriorly in *H. murinus* n. sp. compared to three plates in *H. topapuensis*; **(2)** one short apical seta and one seta of intermediate length on paratergal plate III in *H. murinus* n. sp. compared to two fairly long apical setae on this plate in *H. topapuensis*; **(3)** two apical setae of intermediate length on paratergal plate VI in *H. murinus* n. sp. compared to one short apical seta and one fairly long apical seta on this plate in *H. topapuensis*; **(4)** a distinct lateral protuberance on each side of the pseudopenis in *H. murinus* n. sp.—this is absent in *H. topapuensis*, which has finely crenulated lateral margins on each side of the pseudopenis; **(5)** the smaller size of *H. murinus* (range, 0.62–0.74 mm) compared to *H. topapuensis* (range, 0.83–0.99 mm). Females: **(1)** one row of 4 DCAS immediately preceding the dorsal abdominal plates in *H. murinus* n. sp. compared to 9–10 DCAS in this position in *H. topapuensis*; **(2)** 3–4 DLAS and no VLAS in *H. murinus* n. sp. compared to 10–20 DLAS and 10–20 VLAS in *H. topapuensis*; **(3)** gonopod VIII with four setae in *H. murinus* n. sp. but with three setae in *H. topapuensis*; **(4)** the smaller size of *H. murinus* n. sp. (range, 0.85–1.03 mm) compared to *H. topapuensis* (range, 1.04–1.39 mm).

DESCRIPTION: **Male** (fig. 50A–D). Length of holotype 0.99 mm (mean for series 0.91; range 0.83–0.99, $N = 2$). Head, thorax, and abdomen well sclerotized.

Head. Longer than wide with broadly rounded anterior apex; 2 SuHS, 3 DMHS, 1 DAnCHS, 1 SpAtHS, 2–3 AnMHS, and 1 VPHS on each side; DPHS fairly long, extending to mesothoracic spiracle, with 1 DAcHS medial to DPHS. *Antennae.* 5-segmented with basal segment much wider than second segment, wider than long.

Thorax. Broader than long; thoracic sternal plate (fig. 50B) with broadly rounded anterior apex and tapering, broadly rounded posterior apex; mesothoracic spiracle moderate in size (0.017 mm in diameter); DPTS moderate in length (0.135 mm) almost extending to anterior region of paratergal plate III; 1 DMsS anteromedial to DPTS. *Legs.* Fore and mid-coxae subtriangular; forelegs small each with narrow acuminate claw; hindlegs robust each with broad acuminate claw; midlegs intermediate in size between fore and hind legs.

Abdomen. Wider than thorax; one plate per segment dorsally on segments 7–9; one broad plate per segment ventrally on segments 1 and 2; two plates per segment ventrally on segments 3–7; segment 3 with one broad and one narrow plate ventrally; first row of DCAS with two setae, second and third rows each with 4 DCAS, and rows 4–7 each with 8–10 DCAS, followed by two rows of TeAS each with 6–8 setae and by one row of 2–3 TeAS; 1 DLAS on each of segments 7 and 8; first ventral plate without setae; ventral plates 2–12 each with 4–8 StAS; ventral plates 2 and 3 each articulating with corresponding paratergal plates. *Paratergal plates* (fig. 50C) present on segments 1–8: plate II with one fairly long apical seta and one of intermediate length; plate III with two apical setae of intermediate length; plates IV–VI each with one short apical seta and one of intermediate length; plates VII and VIII each with two long apical setae; all plates subtriangular; plates II–VI each with both apical angles produced into points; plates III–VII each with moderate size spiracle.

Genitalia (fig. 50D). Aedeagal basal apodeme about as long as parameres; parameres curved and tapering posteriorly; pseudopenis short, barely extending beyond apices of parameres; lateral margins of pseudopenis crenulated.

Female (fig. 51A–D). Length of allotype 1.29 mm (mean for series 1.19; range 1.04–1.39; $N = 15$).

Head, *thorax*, and *legs.* As in male unless indicated otherwise. 4 DMHS on each side of head.

Abdomen. Wider than thorax; three plates per segment dorsally on segments 4–6; two plates per segment dorsally on segments 7 and 8; one broad plate ventrally on each of segments 1 and 2; two broad plates ventrally on segment 3; three plates per segment ventrally on segments 4–7; first row of DCAS with two setae, second and third rows each

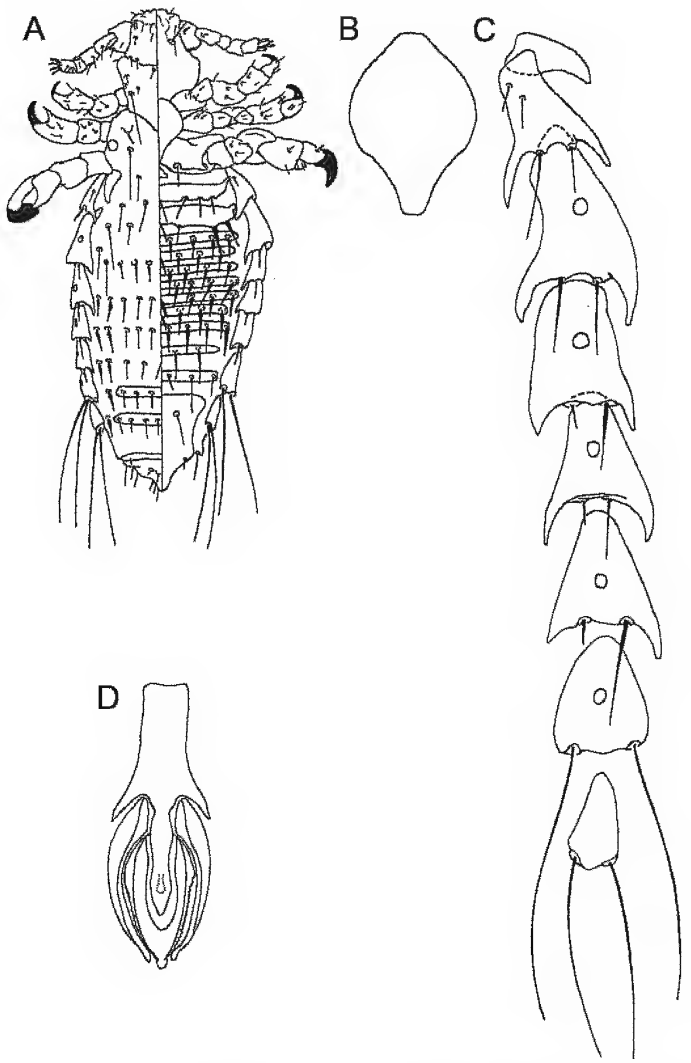

Fig. 50. *Hoplopleura topapuensis*, male. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

with 4 DCAS, row 4 with 8–10 DCAS, followed by 13 rows of TeAS each with 6–9 setae; first ventral plate lacking setae; ventral plates 2–16 each with 6–9 StAS; ventral plates 2 and 3 each articulating with corresponding paratergal plates; rows of 1–2 DLAS and VLAS on segments 4–8. *Paratergal plates* (fig. 51C) as in male except both apical setae on plate III fairly short; plates II–VI subtriangular.

Genitalia (fig. 51D). Subgenital plate with deep lateral indentation on each side; two long lateral setae on each anterior arm of subgenital plate; gonopod VIII with two short medial apical setae and one lateral apical seta of intermediate length; gonopod IX with one stout seta; vulvar fimbriae distinct.

Hoplopleura murinus, new species

HOLOTYPE: Male and allotype female *ex* female *Prosciurillus murinus* (AMNH 226073; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by G.G. Musser at 450 ft at Malakosa, Kuala Navusu

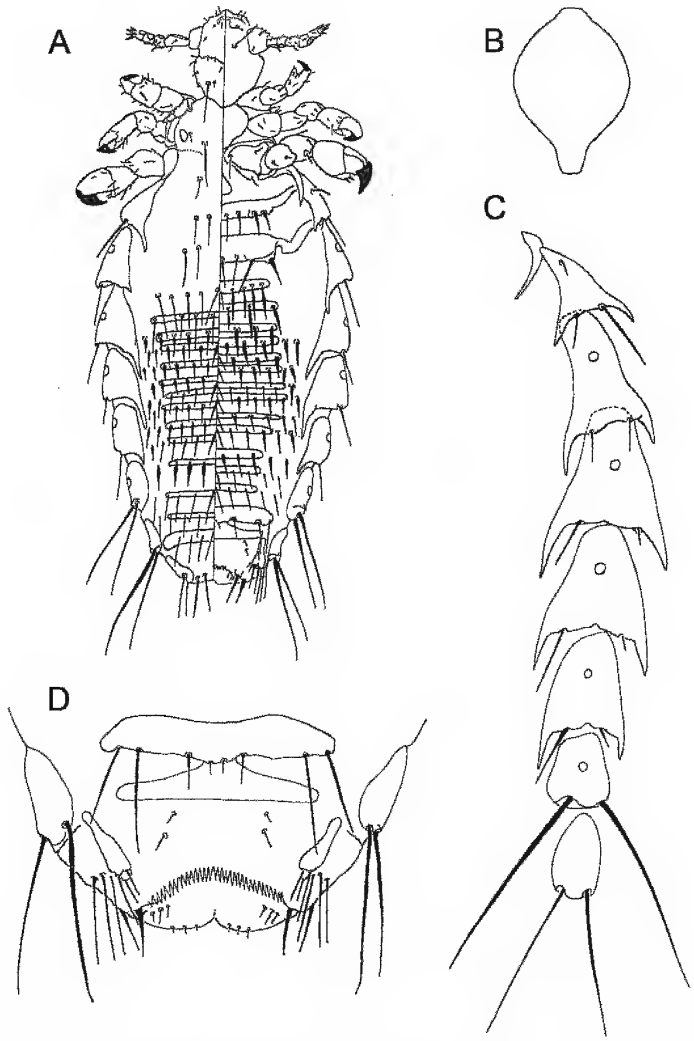

Fig. 51. *Hoplopleura topapuensis*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

(0°58′S, 120°27′E; see gazetteer and fig. 30), Propinsi Sulawesi Tengah, Indonesia on 5 October, 1975. The holotype is deposited in USNM.

REFERRED SPECIMENS: An additional seven males and 21 females from the same host individual as the holotype and allotype; one female *ex* female *P. murinus* (USNM 216794) collected by H.C. Raven at 0–100 m at Teteamoet (1°40′N, 125°05′E), North Sulawesi on 28 January 1916; three males, six females *ex* female *P. murinus* (AMNH 224596) collected by G.G. Musser at 2700 ft at Sungai Sadaunta (1°23′S, 119°58′E), central Sulawesi on 26 September, 1974.

DISTRIBUTION: *Hoplopleura murinus* has been collected from voucher hosts of *Prosciurillus murinus* from both the northern peninsula and central core of Sulawesi. The squirrel host is found in lowland and montane forest habitats throughout Sulawesi (see fig. 11 and table 4).

ETYMOLOGY: This species is named for the specific epithet of its host.

DIAGNOSIS: *Hoplopleura murinus* can be distinguished from all other species of *Hoplopleura* using a combination of the following

characters: **(1)** the presence of five dorsal abdominal plates situated posteriorly in the male; **(2)** the shape of the thoracic sternal plate in both sexes; **(3)** the shape of the paratergal plates and the lengths of the apical paratergal setae in both sexes; **(4)** the shape, setation, and proportions of the male and female genitalia. *Hoplopleura murinus* appears to be most similar to *Hoplopleura topapuensis*; key differences between these two new anopluran taxa are discussed in the descriptive section on *H. topapuensis*.

DESCRIPTION: **Male** (fig. 52A–D). Length of holotype 0.74 mm (mean for series 0.69; range 0.62–0.76; $N = 11$). Head, thorax, and abdomen well sclerotized.

Head. Longer than wide with broadly rounded anterior apex; 2 SuHS, 4 DMHS, 1 DAnCHS, 1 DPoCHS, 1 SpAtHS, 2 DPaHS, 1 VPHS, and 3–4 AnMHS on each side; DPHS fairly long with 1 DAcHS medial to DPHS. *Antennae.* 5-segmented with basal segment wider than second segment, wider than long.

Thorax. Broader than long; thoracic sternal plate (fig. 52B) tapering to blunt anterior apex and to more acute posterior apex; mesothoracic spiracle fairly small (0.014 mm in diameter); DPTS moderate in length (0.105 mm) extending to anterior region of third paratergal plate; one small DMsS medial to spiracle. *Legs.* Hind coxae with spurlike posterior projection; fore and mid coxae subtriangular, each with three small setae; forelegs fairly small each with narrow acuminate claw; hindlegs robust, each with large acuminate claw; midlegs intermediate in size between fore and hindlegs.

Abdomen. Wider than thorax; one broad plate per segment dorsally on segments 5–8; one broad plate per segment ventrally on plates 1–3; two narrow plates per segment ventrally on segments 4–7; five rows of DCAS dorsally—row 1 with 2 DCAS, rows 2 and 3 each with 4–5 DCAS, and rows 4 and 5 each with 6–8 DCAS, followed by four rows of TeAS with 5, 5, 5, and 1 setae, respectively; first ventral plate lacking setae; second ventral plate with 8 StAS; third ventral plate with 6 StAS including two large lateral setae on each side (three on one side in holotype); ventral plates 2 and 3 each articulating with corresponding paratergal plate; ventral plates 4–11 each with 5–10 StAS; some dorsal and ventral abdominal setae dagger-shaped. *Paratergal plates* (fig. 52C) present on segments 1–8: plate I without setae; plate II with one fairly long apical seta and one seta of intermediate length; plates III–V each with one short apical seta and one seta of intermediate length; plate VI with two apical setae of intermediate length; plates VII and VIII each with two long apical setae; plates II–VII subtriangular; plates II–VI each with both apical angles produced into points; plates III–VII each with moderate size spiracle.

Genitalia (fig. 52D). Aedeagal basal apodeme about same length as parameres; parameres curved with differential sclerotization; pseudopenis barely extending beyond apices of parameres, with small lateral protuberance on each side.

Female (fig. 53A–D). Length of allotype 0.94 mm (mean for series 0.94; range 0.85–1.03; $N = 27$).

Head, thorax, and *legs.* As in male unless indicated otherwise. DPTS length 0.113 mm. Thoracic sternal plate (fig. 53B) similar in both sexes but anterior apex more acute in most female specimens.

Abdomen. Wider than thorax; three narrow plates per segment dorsally on segments IV–VIII; 1 broad plate ventrally on each of segments 1–3; three narrow plates per segment ventrally on segments IV–VII; first row of dorsal setae with 2 DCAS, second and third dorsal rows each with 4 DCAS, followed by 15 rows of 5–9 TeAS; few DLAS present; first ventral plate lacking setae, second ventral plate with 8 StAS, third ventral plate with 9 StAS (including two longer, robust setae on each side), and following ventral plates each with 7–10 StAS; ventral plates 2 and 3 each articulating with corresponding paratergal plate; some dorsal and ventral abdominal setae dagger-shaped. *Paratergal plates* (fig. 53C) present on segments 1–8: plate I lacking setae; plates II and IV–VI each with one short apical seta and one seta of intermediate length; plate III with two apical setae of intermediate length; plates VII and VIII each with two long apical setae; plates II–VIII subtriangular; plates III–VII each with moderate size spiracle.

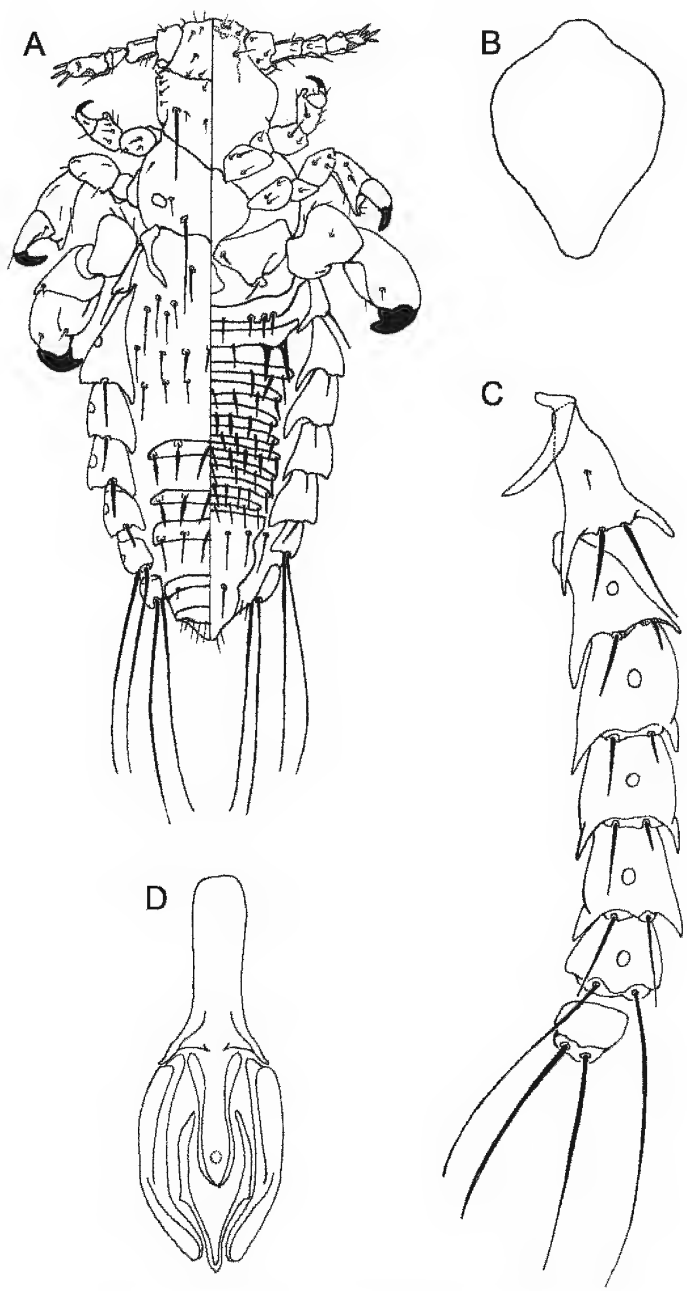

Fig. 52. *Hoplopleura murinus*, male. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

Genitalia (fig. 53D). Subgenital plate with deep lateral indentation on each side; two long setae on each anterior arm of subgenital plate, and four short central setae between these; gonopod VIII with three short apical setae and one subapical seta of intermediate length; gonopod IX with one stout seta; vulvar fimbriae distinct.

REMARKS: Like its squirrel host, *Prosciurillus murinus*, this louse is smaller in body size than its Sulawesian congeners that parasitize other species of Sulawesian squirrels.

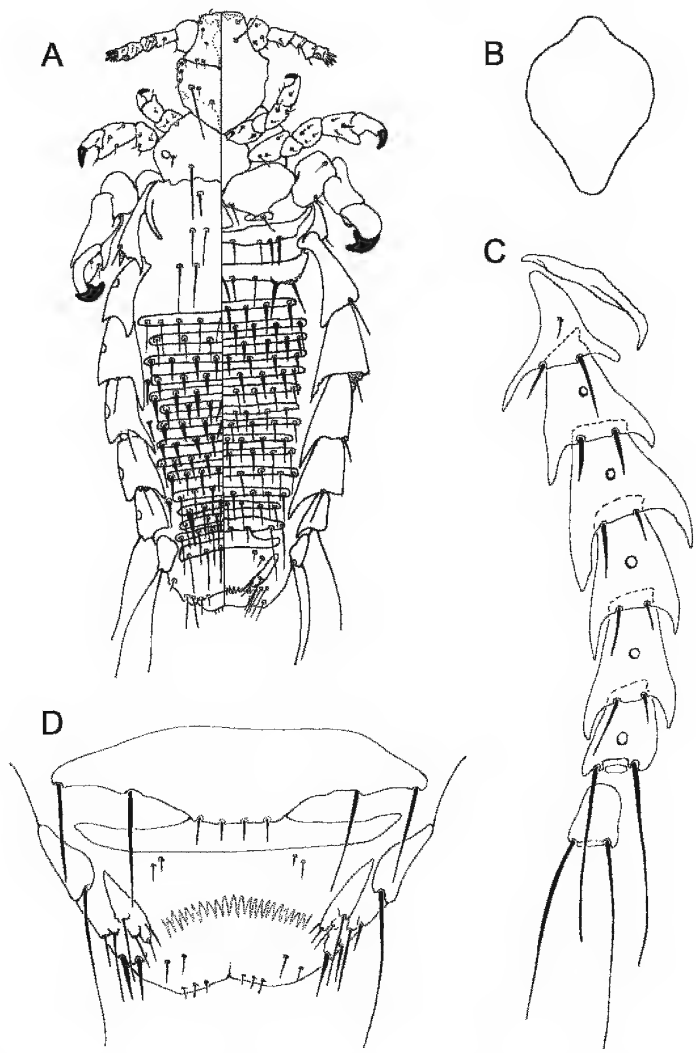

Fig. 53. *Hoplopleura murinus*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

Hoplopleura abstrusus, new species

HOLOTYPE: Male *ex* male *Prosciurillus abstrusus* (AMNH 101359; Rodentia: Sciuridae: Nannosciurinae, Nannosciurini, Hyosciurina) collected by G. Heinrich at 2000 m at Tanke Salokko (3°40′S, 121°13′E; see gazetteer and fig. 30), Pegunungan Mekongga on the southeastern peninsula of Sulawesi (Propinsi Sulawesi Tenggara), Indonesia on 18 December, 1931. The holotype is deposited in USNM.

REFERRED SPECIMENS: The following additional specimens, all collected by G. Heinrich on various dates during December 1931 from the same host species at the same location as the holotype: an additional male, four females, one nymph from the same host individual as the holotype; one nymph *ex* male *P. abstrusus* (AMNH 101349) at 2000 m; three females *ex* male *P. abstrusus* (AMNH 101350) at 1500 m; two females, three nymphs *ex* male *P. abstrusus* (AMNH 101352) at 2000 m; two females *ex* female *P. abstrusus* (AMNH 101353) at 2000 m; one male, two females (including allotype), one nymph *ex* female *P. abstrusus* (AMNH 101354) at 2000 m; four females *ex* male *P.*

abstrusus (AMNH 101355) at 2000 m; one male *ex* male *P. abstrusus* (AMNH 101358) at 2000 m; two males, five females, three nymphs *ex* male *P. abstrusus* (AMNH 101360) at 2000 m; two females, one nymph *ex* male *P. abstrusus* (AMNH 101361) at 2000 m; one male, three females, one nymph *ex* sex unknown *P. abstrusus* (AMNH 101362) collected at 2000 m. Paratypes are deposited in AMNH, BMNH, LAD, and USNM.

DISTRIBUTION: All collections of *Hoplopleura abstrusus* are from *Prosciurillus abstrusus* collected from Tanke Salokko, Pegunungan Mekongga, on the southeastern peninsula of Sulawesi at 1500 m or 2000 m. The tree squirrel is endemic to this mountain range (see fig. 11 and table 4).

ETYMOLOGY: The specific epithet of the host has been used to name this louse.

DIAGNOSIS: *Hoplopleura abstrusus* can be distinguished from all other species of *Hoplopleura* using a combination of the following characters: **(1)** four rows of dorsal abdominal setae followed by five dorsal abdominal plates in the male; **(2)** characteristically shorter, stout setae in some rows of dorsal abdominal setae; **(3)** morphology of the male genitalia, especially the pseudopenis which has lateral projections, and also extends well beyond the apices of the parameres; **(4)** four rows of DCAS followed by 13 dorsal abdominal plates in the female; **(5)** setal lengths on gonopod VIII in the female; **(6)** shape of the subgenital plates in both sexes; **(7)** shape and setation of the paratergal plates in both sexes.

DESCRIPTION: **Male** (fig. 54A–D). Length of holotype 0.93 mm (mean for series 0.91, range 0.87–0.94, $N = 7$). Head and thorax well sclerotized.

Head. Longer than wide with broadly rounded, anterior apex; 2 SuHS, 4 DMHS, 1 DAnCHS, 1 DPoCHS, 3 SpAtHS, 2–3 DAnMHS, and 1 OrS on each side. DPHS short, barely extending beyond posterior margin of head with 1 DAcHS medial to DPHS. *Antenna* 5-segmented with basal segment wider than second segment, much wider than long; second segment elongate.

Thorax. Broader than long; thoracic sternal plate (fig. 54B) blunt anteriorly and tapering to rounded posterior apex; mesothoracic spiracle small (0.015 mm in diameter) with one long DMsS and one DPTS of moderate length (0.11 mm) medial to spiracle. *Legs.* Forelegs and midlegs small each with narrow, acuminate claw; hindlegs and hind claws robust.

Abdomen. Wider than thorax; five rows of DLAS/DCAS anteriorly: rows 1 and 2 each with two setae, rows 3 and 4 each with four setae, row 5 with 8–10 setae; five dorsal plates posterior to DLAS/DCAS rows: plates 1–4 each with 7–12 TeAS, plate 5 without setae; 1–2 DLAS on segments 4–6; some dorsal abdominal setae characteristically peg-like or dagger-like; 11 ventral abdominal plates: plate 1 small and lacking setae, plates 2–11 each with 6–8 StAS, plates 2 and 3 each extending laterally to articulate with corresponding paratergal plate as characteristic of genus, plate 3 with 2 elongate lateral StAS on each side; 1 VLAS on each of segments 3–7 or 3–8. *Paratergal plates* (fig. 54C) present on segments 1–8: plate I lacking setae; plates II and III each with 2 apical PrS of intermediate length; plates IV–VI each with 1 short apical PrS and 1 PrS of intermediate length; plates VII and VIII each with 2 long apical PrS; plates II–VI subtriangular and with both apices developed into points; plates III–VII each with moderate-size spiracle.

Genitalia (fig. 54D). Subgenital plate with small lateral ridge and four long anterior setae on each side (as shown in fig. 54A); aedeagal basal apodeme almost twice as long as parameres; parameres curved and with sinuous medial margins; pseudopenis very long, extending well beyond apices of parameres, with small protuberance on each lateral margin proximal to apices of parameres.

Female (fig. 55A–D). Length of allotype 1.14 mm (mean for series 1.16, range 0.95–1.40, $N = 27$).

Head, thorax, and *legs.* As in male.

Abdomen. Wider than thorax; four rows of setae dorsally with 2, 4, 4, and 8 setae, respectively, followed by 13 dorsal plates each with 5–10 TeAS; plate 13 broad; 1–2 DLAS on each of segments 3–7, 4–7, or 3–8; 17 plates (excluding subgenital plate) ventrally: plate 1 small and lacking setae, plates 2–17 each with 5–8 StAS, plates 2 and 3 each articulating laterally with corresponding

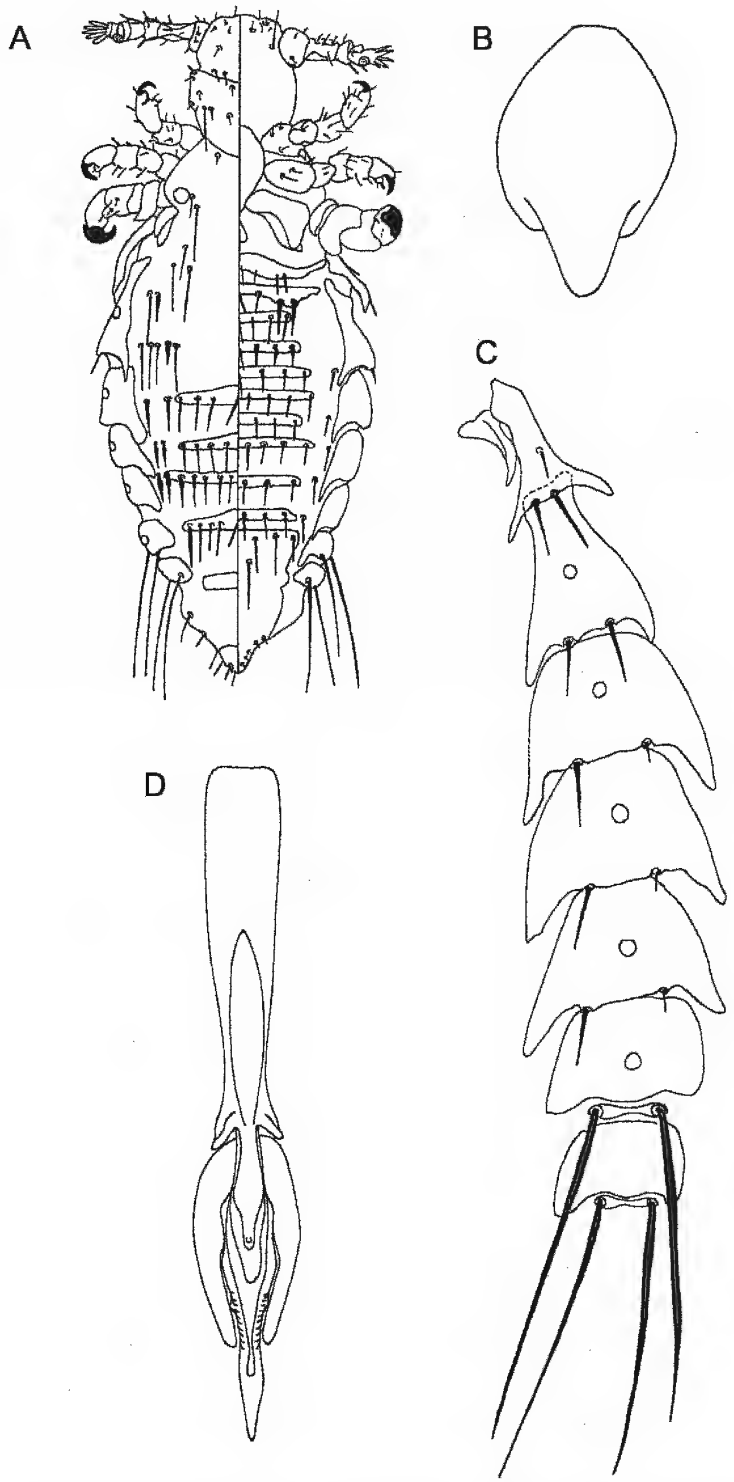

Fig. 54. *Hoplopleura abstrusus*, male. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

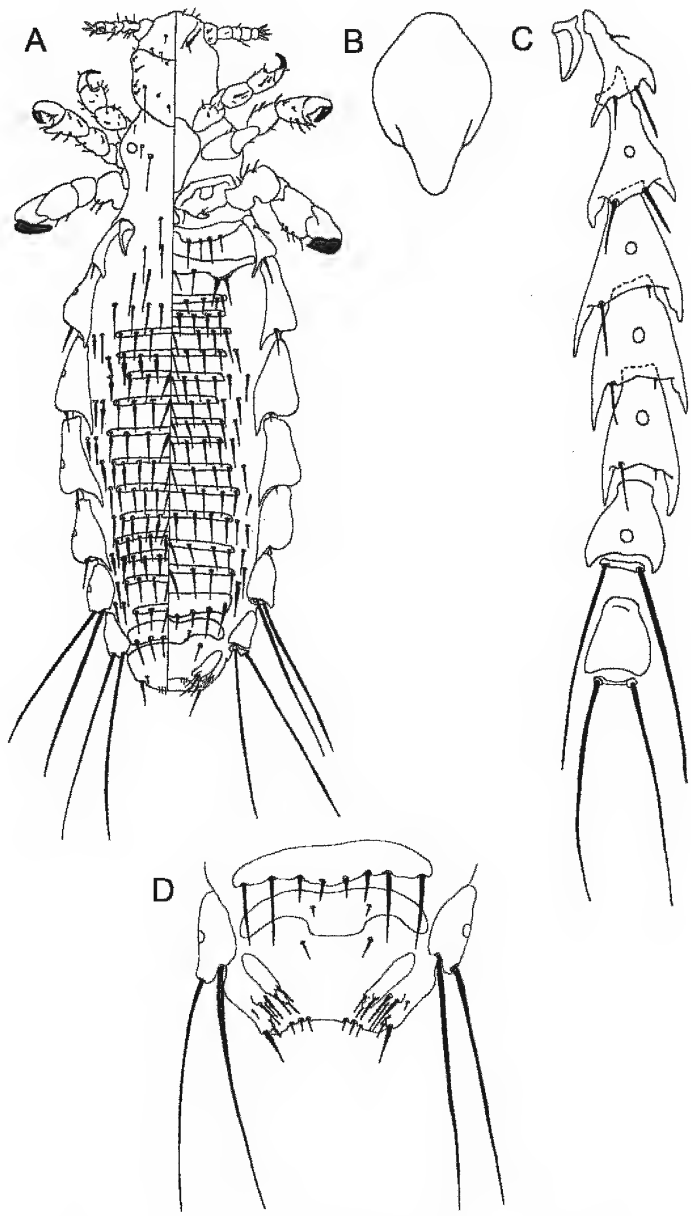

Fig. 55. *Hoplopleura abstrusus*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

paratergal plate as characteristic of genus, plate 3 with two enlarged lateral StAS on each side; 1–2 VLAS present on each of segments 3–7, or 4–7; some TeAS, DLAS, StAS, and VLAS dagger shaped. *Paratergal plates* (fig. 55C) with apical PrS as in male except for one elongate apical PrS on plate II; plates II–VIII subtriangular; plates II–VII each with both apices developed into points; plates III–VII each with moderate-size spiracle.

Genitalia (fig. 55D). Subgenital plate with distal ends curved posteriorly, and with central posterior projection; one small seta on each side of midline on plate and immediately posterior to plate; gonopod VIII

with three apical, posterior setae of short to intermediate length each borne on small lobe; gonopod IX with one robust seta of intermediate length; vulvar fimbriae indistinct.

REMARKS: The very long pseudopenis of the male of *Hoplopleura abstrusus* clearly distinguishes this species from all other species of *Hoplopleura* that parasitize Indomalayan squirrels.

Hoplopleura heinrichi, new species

HOLOTYPE: Male and allotype female *ex* male *Hyosciurus heinrichi* (AMNH 225477; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by G.G. Musser at 7500 ft (2287 m) on Gunung Nokilalaki (1°16′S, 120°10′E; see gazetteer and fig. 35), Propinsi Sulawesi Tengah, Indonesia on 21 March, 1975. The holotype is deposited in USNM.

REFERRED SPECIMENS: An additional female specimen from the same pelt as the holotype and allotype; one female *ex* female *Hyosciurus heinrichi* (AMNH 225486) collected by G.G. Musser at 5100 ft (1555 m) on Gunung Kanino (1°17′S, 120°08′E), central Sulawesi on 13 May, 1975; one female *ex* sex unknown *Hyosciurus heinrichi* (AMNH 101309) collected by G. Heinrich at 2200 m on Pegunungan Latimojong (3°31′S, 119°56′E), in the central core of Sulawesi on 10 June, 1930; one female *ex* female *Hyosciurus heinrichi* (BM 40.650 No. 7a) collected by W.J.C. Frost at 4200 ft on "Molengraff Range [= Pegunungan Takolekaju, see gazetteer] Mid. Celebes" in December, 1938; one male *ex* female *Hyosciurus heinrichi* (BM 40.691b) collected by W.J.C. Frost (date and elevation not given) at "Talamanti [= Tamalanti, see gazetteer], W. Celebes"; one male, one female *ex* male *Hyosciurus heinrichi* (BM 40.644 No. 10a) collected by W.J.C. Frost (date and elevation not given) on "Molengraff Range [= Pegunungan Takolekaju], Mid. Celebes." Paratypes are deposited in AMNH, BMNH, LAD, and USNM.

DISTRIBUTION: *Hoplopleura heinrichi* has been recorded only from *Hyosciurus heinrichi*, which is endemic to the western mountain block in the central core of Sulawesi (see fig. 35 and table 4).

ETYMOLOGY: The specific epithet of the host has been used to name *Hoplopleura heinrichi*.

DIAGNOSIS: *Hoplopleura heinrichi* can be distinguished from all other species of *Hoplopleura* using the following combination of characters: **(1)** the shape of the thoracic sternal plate; **(2)** the shape and proportions of the male genitalia; **(3)** the shape and setation of the female genitalia; **(4)** the shape and setation of the paratergal plates (one long apical seta and one seta of intermediate length on plate II in both sexes, two apical setae of intermediate length on plates III–VI, and two long apical setae on plates VII and VII in females; both apical setae are progressively longer on plates III–VII in males).

DESCRIPTION: **Male** (fig. 56A–D). Length of holotype 1.01 mm (mean for series 1.02; range 1.01–1.05; $N = 3$). Head, thorax, and abdomen well sclerotized.

Head. Longer than wide with broadly rounded anterior apex; 2 SuHS, 4 DMHS, 1 DAnCHS, 1 tiny DPoCHS, 1 SpAtHS, 1 VPHS, 1 OrS, 2 ApHS, and 3–7 AnMHS on each side; DPHS long, extending to base of DPTS, with one small DAcHS medial to DPHS. *Antenna* 5-segmented with basal segment much larger than second segment, about as wide as long.

Thorax. Broader than long; thoracic sternal plate (fig. 56B) with broadly rounded lateral, anterior, and posterior apices; mesothoracic spiracle moderate in size (0.022 mm in diameter) with one small DMsS medial to spiracle; DPTS (0.141 mm long) extending beyond anterior attachment of paratergal plate II. *Legs.* Mid-coxae subtriangular; forelegs small, each with narrow acuminate claw; hindlegs robust, each with large, relatively narrow, acuminate claw; midlegs (missing except for coxa on one side of holotype) intermediate in size between fore and hindlegs.

Abdomen. Wider than thorax; one plate per segment dorsally on segments 3–8; two plates per segment ventrally on segments 4–6; first row of dorsal setae with 2 DCAS, second and third rows each with 4 DCAS, followed by 6–10 TeAS on plates 1–5; 1 DLAS on each of segments 3–7; some lateral tergal setae and DLAS thickened; first ventral plate without setae; second and third ventral plates each

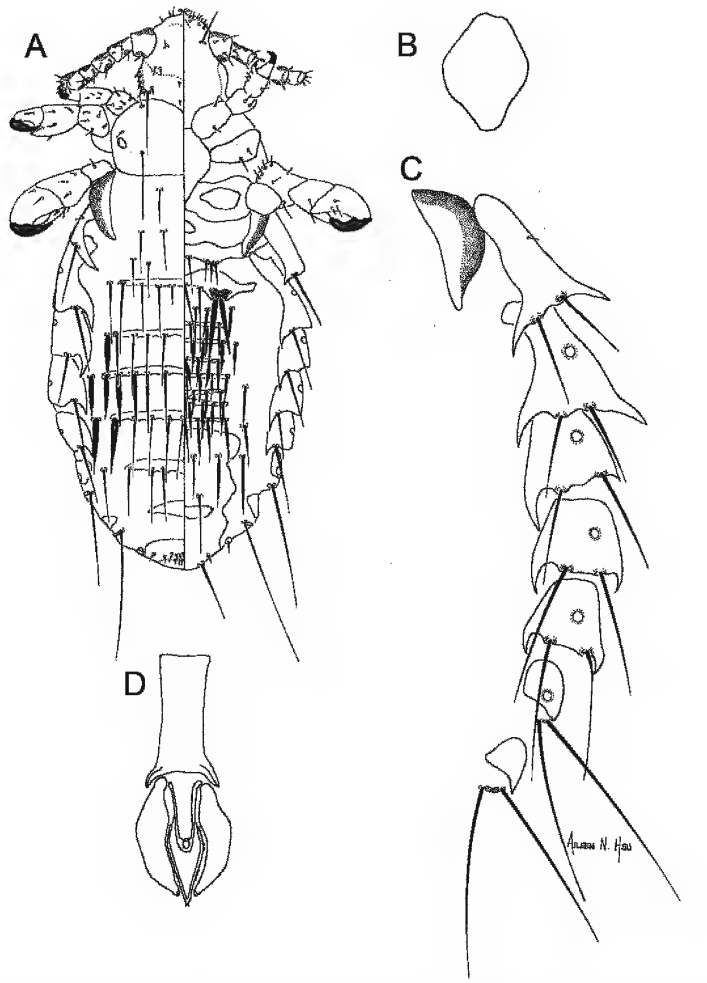

Fig. 56. *Hoplopleura heinrichi*, male. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

with 8 StAS (including two long lateral robust setae on each side on third plate) and partly extending to articulate with corresponding paratergal plates; ventral plates 4–10 each with 6–8 StAS; 1 VLAS on each of segments 3–7. *Paratergal plates* (fig. 56C) present on segments 1–8: plate I without setae; plates II–VIII each with two long apical setae; plates II–IV subtriangular; plates V and VI also subtriangular except for squarish anterior borders; both apical angles of plates II–VI produced into points; plates III–VII each with moderate-size spiracle.

Genitalia (fig. 56D). Aedeagal basal apodeme slightly longer than parameres; parameres curved and tapering apically; pseudopenis extending beyond apices of parameres.

Female (fig. 57A–D). Length of allotype 1.33 mm (mean for series 1.34, range 1.20–1.44, $N = 6$).

Head, thorax, and legs. As in male unless indicated otherwise. 1–2 DAnHS distinct on each side. Thoracic sternal plate (fig. 57B) more elongate than in male and with less distinct lateral apices.

Abdomen. Wider than thorax; one broad plate ventrally on each of segments 1–3; three narrow plates ventrally on each of segments 4–7; one plate dorsally on each of segments 3 and 8; three narrow plates dorsally on each of

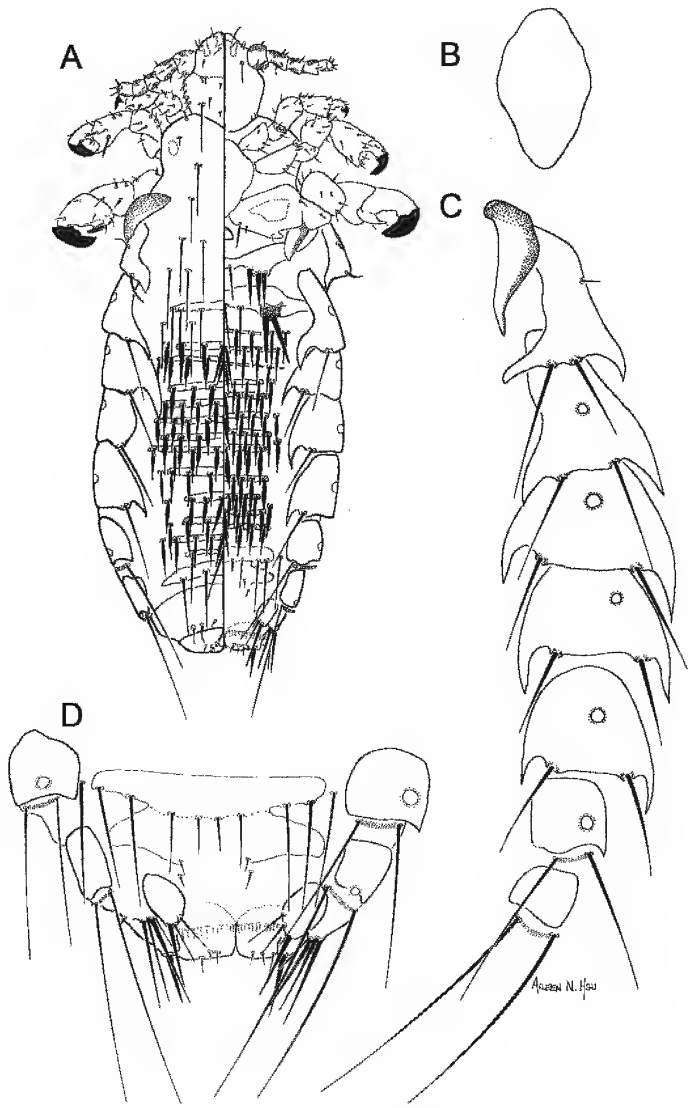

Fig. 57. *Hoplopleura heinrichi*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

segments 4–7; first ventral plate without setae, second ventral plate with 8 StAS, third ventral plate with 7 StAS (including two lateral robust setae on each side), and ventral plates 4–15 each with 6–9 StAS; 2 DCAS in first row of dorsal setae, 4 DCAS in each of dorsal rows 2 and 3, followed by 4–9 TeAS on each dorsal plate; few VLAS and DLAS present; some abdominal setae thickened or dagger-shaped. *Paratergal plates* (fig. 57C) as in male but with both apical setae on plates V and VI of intermediate length and with setae on plate VII shorter than in male.

Genitalia (fig. 57D). Subgenital plate with deep lateral indentation on each side, lightly sclerotized posteriorly; two long setae attached to each anterior arm of subgenital plate and four smaller central setae between these; gonopod VIII with three setae (two medial setae of intermediate length and one

longer and thicker lateral seta); gonopod IX with one long stout seta; vulvar fimbriae evident.

REMARKS: *Hoplopleura heinrichi* is distinct from the new species *Hoplopleura ileile* (see below), a pattern concordant with the presence of two distinctive species within *Hyosciurus*.

Hoplopleura ileile, new species

HOLOTYPE: Female *ex* female *Hyosciurus ileile* (AMNH 224620; Rodentia, Sciuridae, Nannosciurinae, Nannosciurini, Hyosciurina) collected by G.G. Musser at 3150 ft (960 m) at Sungai Sadaunta (1°23′S, 119°58′E; see gazetteer and fig. 35), Propinsi Sulawesi Tengah, Indonesia on 1 November 1974. The holotype is deposited in USNM.

REFERRED SPECIMENS: The following specimens are all from *Hyosciurus ileile* hosts collected in the central core of Sulawesi by G.G., Musser: an additional two nymphs from the same individual as the holotype; two females *ex* male *H. ileile* (AMNH 224618) at 2900 ft (884 m) also at Sungai Sadaunta on 21 October 1974; one female *ex* female *H. ileile* (AMNH 226499) at 1100 ft (335 m) at Tolai, Sungai Tolewonu (1°04′S, 120°27′E) on 31 January 1976; four nymphs *ex* male *H. ileile* (AMNH 223540) at 4800 ft (1463 m) on Gunung Kanino (1°17′S, 120°08′E) on 20 November 1973. Paratypes are deposited in BMNH and LAD.

DISTRIBUTION: *Hoplopleura ileile* is known from voucher hosts collected at only three localities in the northern portion of Sulawesi's central core. Samples of the ground squirrel are from the northern part of the west-central region in the central core and one locality on the northern peninsula (see fig. 35 and table 4).

ETYMOLOGY: *Hoplopleura ileile* has been named for the specific epithet of its host.

DIAGNOSIS: The female of *Hoplopleura ileile* can be distinguished from all other species of *Hoplopleura* by a combination of the following characters: **(1)** the arrangement of the dorsal and ventral abdominal plates and the rows of DCAS and VCAS between these plates; **(2)** the shape of the thoracic sternal plate; **(3)** the shape and setation of the paratergal plates; and **(4)** the shape and setation of the subgenital plate. The female of *Hoplopleura ileile* differs from the female of *Hoplopleura heinrichi* in several characters including the following: **(1)** the shape of the thoracic sternal plate, which is elongate in *Hoplopleura heinrichi* (fig. 57B) but more diamond-shaped with a blunt anterior apex and with distinct lateral apices in *Hoplopleura ileile* (fig. 58B); **(2)** the shape and setation of the paratergal plates, especially the longer apical setae on plate II of *Hoplopleura heinrichi* (figs. 57C and 58C); **(3)** the significant reduction in the number and width of the dorsal and ventral abdominal plates in *Hoplopleura ileile* when compared to *Hoplopleura heinrichi*; **(4)** the presence of rows of DCAS and VCAS between rows of TeAS and StAS in *Hoplopleura ileile* but not in *Hoplopleura heinrichi* (except for a few long setae situated anteriorly on the venter of *Hoplopleura heinrichi*); **(5)** the larger number of dagger-shaped abdominal setae in *Hoplopleura heinrichi*; **(6)** the difference in the shapes of the subgenital plates, especially the deeper lateral indentations in *Hoplopleura ileile*.

DESCRIPTION: **Female** (fig. 58A–D). Length of holotype 1.05 mm (mean for series 1.07, range 1.05–1.09, $N = 4$). Head, thorax, and abdomen fairly well sclerotized.

Head. Longer than wide with broadly rounded anterior apex; 2 SuHS, 4 DMHS (displaced medially in some specimens as in fig. 58A), 1 DAnCHS, 1 DPoCHS, 1 SpAtHS, 1 DPaHS, 2DAnHS, 1 ApHS, 1–2 AnMHS, 1–2 OrS, and 1 VPHS on each side; DPHS moderate in length, just extending to level of thoracic spiracle with 1 DAcHS medial to DPHS. *Antenna* 5-segmented with basal segment wider than second segment, about as wide as long.

Thorax. Broader than long; thoracic sternal plate (fig. 58B) diamond shaped but with blunt anterior apex, moderately rounded posterior apex, and bifid lateral apices; mesothoracic spiracle moderate in size (0.020 mm in diameter) with 1 DMsS medial to spiracle; DPTS moderate in length (0.125 mm in paratypes, broken in holotype), extending to paratergal plate II. *Legs.* Forelegs small with narrow acuminate claw; midlegs and hindlegs progressively larger

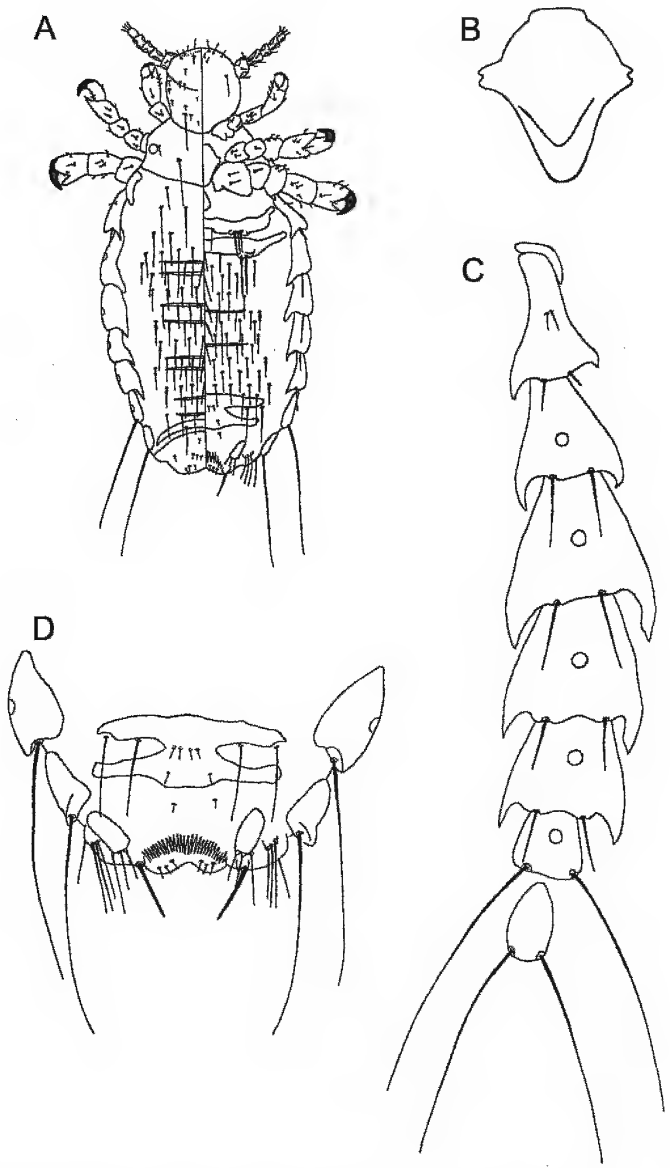

Fig. 58. *Hoplopleura ileile*, female. **A,** dorsoventral view; **B,** thoracic sternal plate; **C,** paratergal plates; **D,** genitalia.

than forelegs with proportionately larger acuminate claws; mid coxae subtriangular.

Abdomen. Wider than thorax with one plate ventrally on each of segments 1–3 and 5–6; one to two narrow plates dorsally on segment 3 and two narrow plates dorsally on segments 4–6; rows of VCAS between StAS; rows of TeAS between pairs of dorsal plates as in figure 58A; first ventral plate without setae, second ventral plate broad, articulating with corresponding paratergal plate, and with 8–10 StAS, including 3–4 (usually three) clustered laterally on each side; third ventral plate also articulating with corresponding paratergal plate but with 7 StAS (including two long, lateral setae on each side); remaining two ventral plates with 4–5 and 5–7 StAS, respectively; rows of 5–8 VCAS present between ventral plates as shown in figure 58A; first row of DCAS with two setae,

second and third rows each with 4 DCAS, and other rows with 5–8 DCAS between dorsal plates as shown in figure 57A; 2–8 TeAS on each dorsal plate; few VLAS and DLAS present; some posterior VLAS and DLAS dagger shaped. *Paratergal plates* (fig. 58C) present on segments 1–8: plate I small and lacking setae; plate II with two short apical setae of subequal length; plates III–VI each with two apical setae of intermediate length; plates VII and VIII each with two long apical setae; plates II–VIII subtriangular; plates III–VII each with moderate-size spiracle.

Genitalia (fig. 58D). Subgenital plate with deep lateral indentation on each side, lightly sclerotized posteriorly; two long setae on each anterior arm of subgenital plate, and 3–4 small central setae between these; gonopod VIII with three setae with lateral seta longer than medial and central setae; gonopod IX with one long stout seta.

REMARKS: The presence of two species of sucking lice on the two host species, *Hyosciurus heinrichi* and *Hyosciurus ileile*, augments the morphological and morphometric data that provide support for the phenetic and taxonomic separation of the hosts. As a group, lice associated with mammals typically phyletically track their hosts (Kim, 1985, 1988; Lyal, 1986, 1987; Grimaldi and Engel, 2005; Light and Hafner, 2007; Smith et al., 2008) so that host speciation often (in about 80% of known cases) also results in louse speciation (Fahrenholz's Rule). Because *Hoplopleura heinrichi* and *Hoplopleura ileile* are distinct taxa and provide important inferences for the taxonomy of their hosts, we felt that both lice should be described in this paper despite the availability of only females and nymphs for the latter species. Nevertheless, two third-instar nymphs of *Hoplopleura ileile* that were preserved just prior to molting to adult males were available and it was from these pharate males (clearly visible beneath the nymphal cuticle) that we assessed male characters for cladistic analyses.

With the species of *Hoplopleura* from the Sulawesi squirrels named and described, the next step is to discuss them in three contexts. First, we provide results of our analysis of the phylogenetic relationships among the Sulawesi louse species and other species of *Hoplopleura* on Indomalayan squirrels. Second, we place the Sulawesi *Hoplopleura* within a portrayal of global sciurid-Anoplura associations. Finally, we use the information presented within the frameworks of the first and second contexts to describe zoogeographic patterns formed by the genera of Anoplura infesting Indomalayan squirrel faunas. The following three sections cover these subjects.

PHYLOGENETIC RELATIONSHIPS AMONG SULAWESI SQUIRREL LICE

Six of the eight new species of lice described in this report form a compact group of geographically and host-defined ectoparasites that are well suited for phylogenetic analysis based on cladistic principles. The 43 characters examined and analyzed for plesiomorphic or apomorphic states are listed in table 52. Characters were obtained for males and females of all the six species of lice. The male characters for *Hoplopleura ileile* were assessed from pharate specimens visible beneath the cuticle of third-instar nymphs preserved immediately before their molt to adult males. Samples of *Hoplopleura leucomus* and *H. alstoni* could not be included in the analysis because they did not contain adult or pharate males. Appendix 1 is a data matrix for the 43 characters examined with 0 denoting plesiomorphy and 1, 2, and 3 reflecting successive apomorphic states.

In addition to the six species of lice parasitic on the endemic Sulawesi squirrels, we included morphological characters of lice from four other species of squirrel hosts and four louse species parasitizing endemic Sulawesi murid rodents. Of the squirrel lice, *Hoplopleura trispinosa* parasitizes the North American flying squirrels, *Glaucomys volans* and *G. sabrinus*, and was employed as an outgroup in the analysis. *Hoplopleura distorta* from *Tamiops swinhoei*, *H. thurmanae* from *Tamiops macclellandi*, and *H. erismata* from species of *Callosciurus* represented lice parasitizing species of Indomalayan squirrels found outside Sulawesi (see table 54). We restricted our sample of *Hoplopleura* to those species parasitizing species of squirrels in Nannosciurini (of Nannosciurinae), which excluded other Indomalayan squirrel species

TABLE 52

Morphological Characters Assessed for Cladistic Analysis of Sulawesi Squirrel Lice and Related Lice[a,b]

(0 = plesiomorphic state; 1, 2, and 3 = successive apomorphic states).

CHARACTERS:

1. Total body length of male more than 1.2 mm (0), 0.8–1.2 mm (1), or less than 0.8 mm (2).

Head

2. Anterior apex of head angular/rounded (0), or broadly flattened (1).
3. Antennae 5-segmented (0) or 4-segmented (1).
4. First antennal segment without (0), or with (1) spinelike seta.
5. Postantennal angle rounded (0), or angular (1).
6. Postantennal angle directed laterally (0), or anterolaterally (1).
7. Postantennal angle lightly (0), or heavily (1) sclerotized.
8. 3 SHS (0), 2 SHS (1), or 1 SHS (2) on each side.
9. Female with 4 DMHS (0), 3 DMHS (1), 2 DMHS (2), or 0 DMHS (3).
10. DPHS situated on lateral lobe (0), or not (1).
11. DPHS long (0), or short (1).

Thorax

12. DPTS long (0), short (1), or absent (2).
13. Mesothoracic spiracle small (0), or large (1).
14. Anterior and posterior processes of thoracic sternal plate dissimilar (0), or similar (1).
15. Posterior apex of thoracic sternal plate elongate (0), broadly rounded (1), or doubled (2).
16. Bladderlike outgrowths absent (0), or present (1) on legs.

Abdomen

17. Abdomen with long (0), or short (1) setae.
18. Second sternite short or absent (0), extended laterally to articulate with corresponding paratergal plate and entire (1), or enlarged and divided medially (2).
19. Sternal abdominal setae uniform (0), or some modified into spiniform or lanceolate forms (1).
20. Tergal abdominal setae uniform (0), or some modified into spiniform or lanceolate forms (1).
21. First TeAS long (0), or short (1).
22. Lateral StAS of segment 3 distinctly enlarged (0), slightly enlarged (1), or not enlarged (2) compared to adjacent setae.
23. Lateral StAS of segment 3 tripled (0), or doubled (1) on each side.
24. Average number of paired DLAS in female more than 20 (0), 8–20 (1), or less than 8 (2).
25. Abdominal sternites on segments 4–7 in male well-developed (0), or poorly developed (1).
26. Abdominal tergites on segments 4–7 in male well-developed (0), poorly developed (1), or absent (2).
27. Abdominal tergite on segment 3 in male without (0), or with (1) distal lobe.
28. Distal end of female abdomen without (0), or with (1) distinct protuberances each bearing an elongate seta to collectively form a "comblike" structure.

Paratergal plates

29. Spiracles associated with 6 pairs (0), 5 pairs (1), or 3 pairs (2) of paratergal plates.
30. Diameter of spiracles IV–VI small (0), or large (1).
31. Paratergal plate II with 2 long apical setae (0), with 1 long and 1 short apical seta (1), with 2 short apical setae (2), or with 1 seta (3).
32. Paratergal plate II not appreciably elongate (0), or greatly elongate as a "winglike" appendage (1).
33. Paratergal plates III–VI with both apical setae of similar lengths (0), or of contrasting lengths (1).
34. Paratergal plates VII and VIII of female symmetrical (0), or asymmetrical (1).

Female genitalia

35. Female gonopod VIII with long (0), or short (1) setae.
36. Female subgenital plate well sclerotized (0), or poorly sclerotized (1).
37. Female subgenital plate without (0), or with (1) deep lateral indentation on each side.

Male genitalia

38. Margins of male subgenital plate smooth (0), or scalloped (1).
39. Male basal apodeme longer than (0), or about equal in length (1) to parameres.
40. Parameres uniformly (0), or differentially (1) sclerotized.

TABLE 52
(Continued)

CHARACTERS:

41. Medial margins of parameres smooth (0), or with a spinelike projection (1).
42. Pseudopenis extending well beyond the apices of the parameres (0), or not (1).
43. Lateral margins of pseudopenis smooth (0), with fine crenulations (1), or with a spinelike projection (2).

[a]Some uninformative characters were informative when different outgroup taxa were included in the matrix (data available upon request).

[b]Synopsis of species of *Hoplopleura* from which morphological traits were surveyed and employed in the data matrix and cladogram (all known species of *Hoplopleura* that parasitize species of squirrels in the Nannosciurini are included in the analysis): **(1)** *H. trispinosa*: outgroup; parasitizes species of *Glaucomys* in North America. **(2)** *H. distorta*: parasitizes *Tamiops swinhoei* in China. **(3)** *H. erismata*: parasitizes species of *Callosciurus* on mainland Southeast Asia (Myanmar, India, Nepal, peninsular Malaysia, China, and Thailand). **(4)** *H. thurmanae*: parasitizes species of *Tamiops* and *Menetes berdmorei* in China and Thailand. **(5)** *H. abstrusus*: parasitizes *Prosciurillus abstrusus* in Sulawesi. **(6)** *H. heinrichi*: parasitizes *Hyosciurus heinrichi* in Sulawesi. **(7)** *H. ileile*: parasitizes *Hyosciurus ileile* in Sulawesi. **(8)** *H. murinus*: parasitizes *Prosciurillus murinus* in Sulawesi. **(9)** *H. rubrisciuri*: parasitizes *Rubrisciurus rubriventer* in Sulawesi. **(10)** *H. topapuensis*: parasitizes *Prosciurillus topapuensis* in Sulawesi. **(11)** *H. chrysocomi* parasitizes *Bunomys chrysocomus* in Sulawesi. **(12)** *H. musseri* parasitizes *Maxomys musschenboekii* in Sulawesi. **(13)** *H. sembeli* parasitizes *Maxomys hellwaldii* in Sulawesi. **(14)** *H. traubi* parasitizes *Maxomys wattsi* in Sulawesi.

in other tribes (Indian *Funambulus* in Funambulini of Nannosciurinae, for example, and Chinese *Sciurotamias* in Marmotini of Xerinae).

Because most representatives of *Hoplopleura* parasitize murid rodents (Durden and Musser, 1994) and secondarily infest sciurids (representing host switching), we also employed in the analysis characters from four species of *Hoplopleura* recorded only from endemic Sulawesi rats (Muridae). *Hoplopleura chrysocomi* is specific to its host, *Bunomys chrysocomus* (Durden, 1990); *H. sembeli* is mainly a parasite of *Maxomys hellwaldii* but a few specimens have been collected from *Bunomys fratrorum* and *Rattus hoffmanni* (Durden, 1990); *H. musseri* is host-specific to *Maxomys musschenbroekii* (Durden, 1990); *H. traubi* paratisizes *Maxomys wattsi* (Durden and Musser, 1991). Including these four murid lice and the six squirrel lice, all endemic to Sulawesi, would help test the cladistic relationship of the squirrel parasites, whether they were recovered as a monophyletic cluster or instead intermingled with the murid-associated species of lice.

Of the 43 characters examined, 32 were potentially parsimony informative. MP analysis produced two equally parsimonious trees (length, 101; consistency index [CI], 0.426; retention index [RI], 0.525; rescaled consistency index [RC], 0.223; fig. 59). Bayesian analyses yielded a similar, although generally less resolved, tree (fig. 59; Bayesian topology available upon request). Bootstrap and Bremer support values and Bayesian posterior probabilities were generally small (fig. 59). The MP analysis resulted in a monophyletic clade of Sulawesi squirrel lice (Bayesian posterior probability = 0.60, Bremer support = 2; fig. 59) distinct from a monophyletic clade of Sulawesi murid lice (Bayesian posterior probability = 0.68, Bremer support = 2; fig. 59)

Reconciliation analyses using TreeMap 2.0β did not support significant phylogenetic congruence between squirrel lice and their hosts for all combinations of host species relationships ($P > 0.3$). There are two phylogenetic incongruities within the squirrel-louse cladogram. One is the position of *Hoplopleura rubrisciurus*, which parasitizes the tree squirrel *Rubrisciurus rubriventer*, nested in the clade containing *H. heinrichi* and *H. ileile*, the lice infesting the two species of ground squirrels in *Hyosciurus*. Among the hosts, *Rubrisciurus* is cladistically linked to the tree squirrels in *Prosciurillus* in a clade separate from *Hyosciurus* (Mercer and Roth, 2003). The other phylogenetic incongruity is the association of *H. murinus* (infesting *Prosciurillus murinus*) with *H. topapuensis*

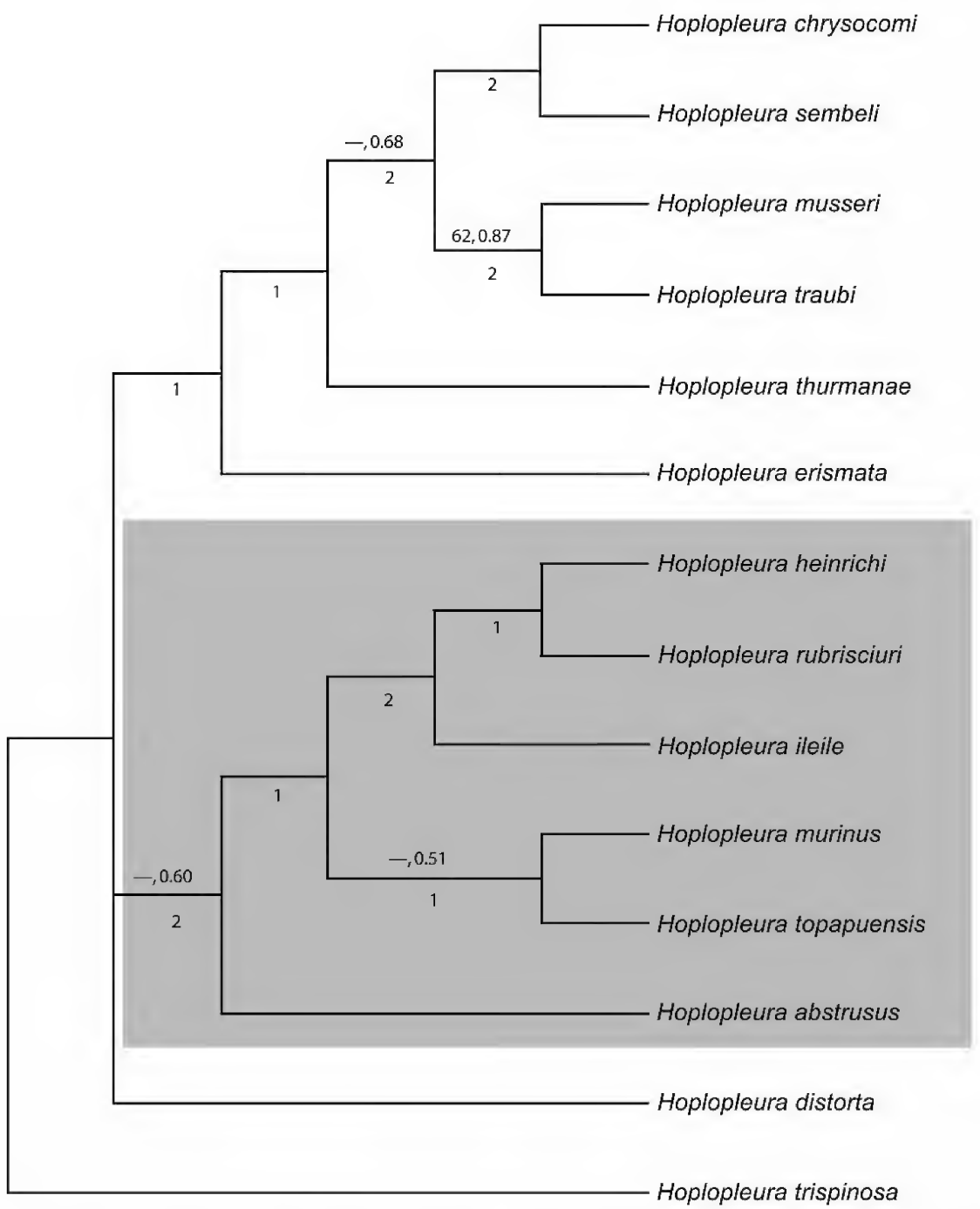

Fig. 59. Maximum parsimony majority rule consensus tree showing phylogenetic relationships among species of *Hoplopleura* from rodent hosts based on 43 morphological characters. Maximum parsimony bootstrap support values and Bayesian posterior probabilities are indicated above the nodes and Bremer support values are given below the nodes. Species of sucking lice parasitizing endemic Sulawesi squirrels form a monophyletic group (indicated in the gray box).

(the louse on *P. topapuensis*). Among species of *Prosciurillus*, *P. murinus* is most closely related to *P. abstrusus* and the two together comprise the *P. murinus* group, while *P. topapuensis* is a member of the larger-bodied *P. leucomus* group (which includes *P. leucomus*, *P. alstoni*, *P. weberi*, and *P. rosenbergii*).

But "Cladograms of hosts and their symbionts are never perfectly congruent ...," and how "... the cladograms match to each other is the result of several 'sorting events': cospeciation, host colonization/shift, intrahost speciation, extinction, or any combination of these" (Grimaldi and Engel, 2005: 278). Such is the imperfect match between cladograms of Sulawesi squirrels and their parasitic lice. Degrees of incongruence are also illustrated in results of the cospeciation studies involving lice and their bird hosts (seabirds in Procelariiformes and Sphenisciformes [Paterson et al., 2000] and swiftlets in Collocallinae [Page et al., 1998]); and even between chewing lice and their pocket gopher hosts (Geomyidae; Hafner et al., 1994; Hafner and Page, 1995), which is probably the "—most intensively studied and well-known example of louse-host cospeciation ..." (Grimaldi and Engel, 2005: 278).

Our results derive from morphological characters possessed by the sucking lice and gene sequences sampled from the hosts. The lice-host cospeciation studies for birds and pocket gophers cited previously employed gene sequences from the bird and rodent lice and from their hosts. Certainly the future step in testing the cospeciation of lice and Sulawesi squirrel hosts and the integrity of our cladogram is to employ sequences from mitochondrial and nuclear genes. At a different level, the significant cladistic pattern shown here describes the six species of *Hoplopleura* from their squirrel hosts as a monophyletic group separate from the other species of *Hoplopleura* employed (that parasitize non-Sulawesi Indomalayan squirrels and endemic Sulawesi murid rodents), which is congruent with the monophyly of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus* relative to the separate clades recovered in other Indomalayan nannosciurine genera (Mercer and Roth, 2003).

A SYNOPSIS OF GLOBAL SCIURID-ANOPLURA ASSOCIATIONS

The new taxa described in this paper represent a significant addition to the sucking louse fauna known to parasitize sciurid rodents and it is appropriate to consider briefly the host associations and zoogeography of currently recognized genera of Anoplura known to parasitize this group of mammals. The hosts and geographical distributions of all 11 genera of Anoplura that are known to parasitize sciurids are listed in table 53. This figure is higher than the number of anopluran genera known to parasitize any other single family of mammals (Durden and Musser, 1994; Kim, 2006), with the next highest figures being six genera (*Hoplopleura*, *Cuyana*, *Eulinognathus*, *Galeophthirus*, *Lagidiophthirus*, and *Polyplax*) associated with rodents in Muroidea (as interpreted by Musser and Carleton, 2005) and Hystricognathi (see Woods and Kilpatrick, 2005), three genera (*Hoplopleura*, *Pterophthirus*, and *Ctenophthirus*) associated with rodents in Echimyidae (infraorder Hystricognathi), and three genera (*Haematopinus*, *Linognathus*, and *Solenopotes*) associated with each of the Bovidae and Cervidae.

All five genera (*Atopophthirus*, *Enderleinellus*, *Microphthirus*, *Phthirunculus*, and *Werneckia*) belonging to the anopluran family Enderleinellidae (representing representing 56 species, including two undescribed species of *Enderleinellus*—one from *Microsciurus flaviventer* in Peru, the other from *Tamiops maritimus* in Laos) are exclusively parasites of sciurids (table 53; Ferris, 1919; Werneck, 1948; Kim and Ludwig, 1978; Chin, 1979; Kim, 1966, 1985, 1988, 2006). There appears to have been significant parallel evolution between the Enderleinellidae and the Sciuridae, with close phyletic host tracking shown by these lice at both the generic and species levels (Kim, 1988, 2006). As a group, the Enderleinellidae is widely distributed within the Ethiopian, Nearctic, Neotropical, Oriental, and Palearctic regions as parasites of squirrels in the tribes Nannosciurini, Funambulini, Protoxerini, Sciurini, and Pteryomyini. However, most of this wide distribution can be attributed to the various species of *Enderleinellus* because

TABLE 53
Genera of Sucking Lice Parasitic on Sciurid Rodents

Louse taxon	Species infesting sciurids (species in genus)	Host; subfamily and (tribe)	Geographic distribution of sciurid-infesting species
Endherleinellidae			
Atopophthirus	2 (2)	*Petaurista*; Sciurinae (Pteromyini)	China, Malay peninsula
Enderleinellus	47 (47)[a]	Nannosciurinae (Nannosciurini and Funambulini), Xerinae (Protoxerini), Sciurinae (Sciurini)	Eurasia, New World,[b] Africa
Microphthirus	1 (1)	*Glaucomys*; Sciurinae (Pteromyini)	North America
Phthirunculus	1 (1)	*Petaurista*; Sciurinae (Pteromyini)	China, Taiwan, Sumatra
Werneckia	5 (5)	Xerinae (Protoxerini)	Africa
Hoplopleuridae			
Hoplopleura	20 (159)[c]	Nannosciurinae (Nannosciurini), Xerinae (Marmotini), Sciurinae (Sciurini and Pteromyini)	North America,[b] southern Asia
Paradoxophthirus	1 (1)	*Sciurotamias*; Xerinae (Marmotini)	China
Polyplacidae			
Johnsonpthirus	5 (5)	Xerinae (Protoxerini)	Africa
Linognathoides	10 (10)	Xerinae (Marmotini and Xerini)	Africa, Eurasia, North and Central America
Neohaematopinus	30 (32)	Nannosciurinae (Nannosciurini), Sciurinae (Pteromyini and Sciurini)	Eurasia, New World[b]
Polyplax	1 (79)	*Spermophilus*: Xerinae (Marmotini)	Bulgaria

[a]Two undescribed species are included in this number, one from a Peruvian squirrel, another from a Laotian species.
[b]*Enderleinellus longiceps*, *Hoplopleura sciuricola*, and *Neohaematopinus sciuri* have accompanied the Nearctic *Sciurus carolinensis* as introductions to various parts of the world.
[c]An undescribed species from a Philippine squirrel is included in this number.

Atopophthirus and the monotypic *Phthirunculus* are confined to Oriental flying squirrels, the monotypic *Microphthirus* parasitizes Nearctic flying squirrels, and the five known species of *Werneckia* occur only on Afrotropical Funambulini and Protoxerini (Durden and Musser, 1994; see also table 53).

Two genera of hoplopleurid sucking lice, *Hoplopleura* and *Paradoxophthirus*, parasitize sciurids (table 53). Most representatives of the numerically large genus *Hoplopleura* parasitize murid rodents (Durden and Musser, 1994) although secondary infestations (representing host switching) such as those of the sciurids listed in table 54, have evidently occurred on a few occasions during the evolution of the Hoplopleuridae. Infestations of sciurids by characteristic species of *Hoplopleura* reflect scenarios where strict phyletic tracking of murid hosts failed to occur and host switching took place instead; other examples of host switching have been discussed in connection with trichodectid chewing lice and their hosts by Lyal (1986, 1987), Hafner and Nadler (1988, 1990), and Page (1990), and for argasid ticks by Klompen et al. (1994). Data included in table 54 suggest that representatives of the genus *Hoplopleura* switched from murids to sciurids as hosts on several separate occasions with present-day descendants of these switches now represented by two species (*H. sciuricola* and *H. trispinosa*) on North American tree squirrels and flying squirrels (subfamily Sciurinae); two species (*H. arboricola* and *H. erratica*) on Nearctic species of chipmunks, and one (*H. xiei*) on a Chinese ground squirrel (subfamily Xerinae; 14 species (*H. abstrusus*, *H. distorta*, *H. erismata*, *H. funambuli*, *H. heinrichi*, *H. ileile*, *H. karachiensis*, *H. maniculata*, *H. murinus*, *H. rubrisciuri*, *H. thurmanae*, *H. topapuensis*, *H. leucomus*, and *H. alstoni*) associated with nannosciurine squirrels in the Indomalayan region. While the three species

TABLE 54
Described Species of *Hoplopleura* Parasitic on Sciurid Rodents[a]

Louse	Host	Subfamily (tribe)	Distribution	Reference
H. abstrusus	*Prosciurillus abstrusus*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. alstoni	*Prosciurillus alstoni*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. arboricola	*Neotamias* spp.	Xerinae (Marmotini)	Central and western North America	Kim et al., 1986
H. distorta	*Tamiops swinhoei*	Nannosciurinae (Nannosciurini)	China	Ferris, 1921, 1951
H. erratica	*Tamias striatus*	Xerinae (Marmotini)	Eastern North America	Kim et al., 1986
H. erismata	*Callosciurus* spp.	Nannosciurinae (Nannosciurini)	Mainland Southeast Asia	Johnson, 1959, 1964
H. funambuli[b]	*Funambulus pennantii*	Nannosciurinae (Funambulini)	Pakistan	Bilquees, 1976
H. heinrichi	*Hyosciurus heinrichi*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. karachiensis[b]	*Funambulus pennantii*	Nannosciurinae (Funambulini)	Pakistan	Khanum, 1983
H. ileile	*Hyosciurus ileile*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. leucomus	*Prosciurillus leucomus*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. maniculata (synonym: *H. mitsuii*)	*Funambulus palmarum*	Nannosciurinae (Funambulini)	Indian subcontinent including Sri Lanka	Mishra, 1981; Durden et al., 1990
H. murinus	*Prosciurillus murinus*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. rubrisciuri	*Rubrisciurus rubriventer*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. sciuricola	*Sciurus* spp.	Sciurinae (Sciurini)	North, Central, and northern South America (introduced elsewhere)	Kim et al., 1986; Durden and Musser, 1994
H. thurmanae	*Tamiops macclellandi*, *Tamiops maritimus*	Nannosciurinae (Nannosciurini)	China, Laos, Thailand	Johnson, 1959
H. topapuensis	*Prosciurillus topapuensis*	Nannosciurinae (Nannosciurini)	Sulawesi	present report
H. trispinosa	*Glaucomys volans*, *Glaucomys sabrinus*	Sciurinae (Pterymyina)	North America	Kim et al., 1986
H. xiei	*Sciurotamias davidianus*	Xerinae (Marmotini)	China	Chin, 1996

[a]An undescribed species of *Hoplopleura* parasitizes *Sundasciurus samarensis* on Biliran Island in the Philippines, and previously undocumented specimens of *Hoplopleura thurmanae* are from *Tamiops maritimus* in Laos.

[b]We have not seen specimens of *Hoplopleura funambuli* and *H. karachiensis* described from *Funambulus pennantii* in Pakistan.

of *Hoplopleura* associated with *Funambulus* parasitize closely related (congeneric) squirrels, hosts of the North American and Indomalayan species of *Hoplopleura* are less intimately related, and more than one host switch from murids to sciurids may have been responsible for present host-louse associations in each region.

Paradoxophthirus emarginata (Ferris), the sole representative of its genus, also was formerly placed in the genus *Hoplopleura* (Ferris, 1922; Durden and Musser, 1994).

However, this louse has several unusual morphological features (including some that are shared with the polyplacid genus *Neohaematopinus*) that led Chin (1989) to erect a new genus for it. *Paradoxophthirus emarginata* is exclusively parasitic on the Chinese ground squirrel *Sciurotamias davidianus*, a member of the tribe Marmotini of subfamily Xerinae that also embraces Nearctic and Palearctic marmots and chipmunks, North American and Eurasian ground squirrels, and North American prairie dogs (see Thorington and Hoffmann, 2005, and our section on classification of squirrels).

Four genera of polyplacid sucking lice parasitize sciurids (table 53). Two of these genera, *Johnsonpthirus* and *Linognathoides*, exclusively parasitize sciurids (Kim and Adler, 1982; Durden, 1991a, 1991b; Durden and Musser, 1994; Kim, 2006). The five described species of *Johnsonpthirus* parasitize African squirrels belonging to *Paraxerus*, *Funisciurus*, and *Heliosciurus* in Protoxerini of Xerinae (Kim and Adler, 1982). Species of *Linognathoides* are parasites of squirrels in Xerinae: Asian, European, and North American Marmotini (marmots and prairie dogs) and African Xerini (Kim and Adler, 1982).

Neohaematopinus is another polyplacid louse genus that primarily parasitizes sciurids with 30 of the 32 described species exclusively associated with rodents belonging to this family (Durden, 1991a; Kim, 2006). The two exceptions, *N. inornatus* and *N. neotomae*, parasitize species of woodrats (*Neotoma*) in North and Central America (Kim et al., 1986; Durden and Musser, 1994) and reflect host switching from sciurid to neotomine rodents. *Neohaematopinus* is mainly a genus of the northern land masses with no native species in Africa (or Antarctica or Australia where suitable hosts would be unavailable anyway) and only two species with ranges that extend partially into the northern Neotropics (Johnson, 1972; Durden, 1991a). However, this louse genus is widespread across North America and Eurasia and it has successfully parasitized numerous species of Indomalayan nannosciurine squirrels (Johnson, 1959, 1964; Durden and Musser, 1994). Some other species of *Neohaematopinus* are associated with squirrels in Sciurini and Pteromyini (Sciurinae).

Although the genus *Polyplax* principally parasitizes murid rodents (Durden and Musser, 1994), one species, *P. bureschi* Touleshkov, infests the common suslik (*Spermophilus citellus*) in Europe (Touleshkov, 1957). This louse-squirrel association apparently represents another case of host switching from the more normal murine-tracking path of *Polyplax* onto a sciurid.

ZOOGEOGRAPHY OF ANOPLURA PARASITIZING INDOMALAYAN SCIURIDS

The geographical distributions and numbers of species present for the seven genera of sciurid-infesting Anoplura in eight Southeast Asian countries, regions, islands, or island-groups traveling southwest from China and Thailand through peninsular Malaysia and then eastwards through the Greater Sunda Islands to Sulawesi and the Philippines are listed in table 55. This approximates the hypothesized migration route that ancestral sciurids traversed during their historical colonization of the Sunda Shelf, Sulawesi, and the Philippines from mainland Southeast Asia (Traub, 1972; Durden and Traub, 1990). Sulawesi and the southern Philippines represent the easterly most extensions of the sciurid colonizations east of the Sunda Shelf. We stress that many areas in the Indomalayan region have been inadequately sampled for sucking lice and forthcoming descriptions of new taxa will necessitate emendations to some of the numbers given in table 55. However, current data clearly show that the three mainland regions all have more known genera and species of sciurid-infesting Anoplura than any of the five islands or island-groups listed. It appears that progressively fewer sucking lice accompanied ancestral sciurids in their colonizations deeper onto the Sunda Shelf, Sulawesi and the Philippines. A similar situation has been described for ceratophyllid fleas parasitizing sciurids and for leptopsyllid fleas infesting murine rodents in the Indomalayan region (Traub, 1983; Durden and Traub, 1990).

The larger number of anopluran genera and species reported from mainland Southeast Asia, particularly China, is also partly related to the greater diversity of potential

TABLE 55
The Known Louse Species in Seven Genera Parasitic on Sciurid Rodents in the Indomalayan Region

Genus	China	Taiwan	Thailand	Malay peninsula	Sumatra	Java	Borneo	Philippines	Sulawesi
Atopophthirus	1	0	0	1	0	0	0	0	0
Enderleinellus	8	1	5	2	0	2	3	0	0
Phthirunculus	1	1	0	0	1	0	0	0	0
Hoplopleura	3	0	2	1	0	0	0	1[a]	8
Paradoxophthirus	1	0	0	0	0	0	0	0	0
Linognathoides	2	0	0	0	0	0	0	0	0
Neohaematopinus	7	2	7	3[b]	1	0	4	1[c]	0
Total species	23	4	14	7	2	2	7	2	8

[a]An undescribed species of *Hoplopleura* known to us parasitizes *Sundasciurus samarensis* on Biliran Island in the Philippines. This species of squirrel also occurs on the nearby islands of Samar and Leyte and is likely conspecific with *S. philippinensis*, the species found on Mindanao and adjacent islands (Thorington and Hoffman, 2005: 788). Biliran, Samar, Leyte, Mindanao, and nearby smaller islands were all part of a single land mass during the Pleistocene: Greater Mindano (Heaney, 1986).

All Philippine sciurids, including those on Palawan, are members of *Sundasciurus*, a Sundaic genus, and although in the same subfamily and tribe as the Sulawesi endemics (Nannosciurinae, Nannosciurini, respectively) they form a monophyletic clade (Nannosciurina) separate from the monophyletic clade containing the Sulawesi species (Hyosciurina); see our section on classification.

[b]Records of the Holarctic *Neohaematopinus sciuri* and the Nearctic *N. sciurinus* from peninsular Malaysia (Kim and Adler, 1982) are erroneous (Durden, 1991a) and are excluded from the table.

[c]*Neohaematopinus sundasciuri* parasitizes *Sundasciurus juvencus* on Palawan Island (Durden, 1991a). Palawan is politically a part of the Philippines but zoogeographically more closely allied with Borneo than with the main clump of islands in the Philippine Archipelago (Heaney, 1986). This zoogeographic relationship is also shown by additional *Neohaematopinus* infestations. Four species of *Neohaematopinus* have been recorded from nine Bornean species of squirrel hosts representing two subfamilies of Sciuridae (Sciurinae and Nannosciurinae): **(1)** *N. callosciuri* parasitizes *Callosciurus nigrovittatus*, *C. notatus*, *C. prevostii*, and *Glyphotes simus*; **(2)** *N. cognatus* is found on *Dremomys everetti*, *Callosciurus jentinki*, and *Nannosciurus whiteheadi*; **(3)** *N. kinabalensis* is associated with *Hylopetes spadiceus* (originally identified as *H. sagitta harrisoni*, but the trinomial is currently associated with *H. spadiceus*; Rasmussen and Thorington, 2008); and **(4)** *N. pansus* infests *Petaurillus hosei*.

No species of *Hoplopleura* is known to infest Bornean squirrels. East of the Malay Peninsula, species of *Hoplopleura* appear as squirrel parasites only on Sulawesi and on Biliran Island in the main Philippines, two regions from which *Neohaematopinus* is apparently absent.

sciurid hosts in these areas (Chin, 1979, 1985, 1989, 1991, 1994; Corbet and Hill, 1992; Thorington and Hoffmann, 2005). For example, marmots are parasitized by sucking lice belonging to *Linognathoides* (and *Enderleinellus* in some other regions) but in continental Asia, marmots do not range farther south than northern China (Chin, 1985; Thorington and Hoffmann, 2005; Hoffman and Smith, 2008). Similarly, *Sciurotamias davidianus*, the sole ground squirrel host of the monotypic anopluran *Paradoxophthirus*, is confined to China (Moore and Tate, 1965; Corbet and Hill, 1992; Hoffman and Smith, 2008). Also, Chin (1979, 1985, 1989, 1991, 1994) has intensively surveyed the Chinese sucking louse fauna, while Johnson (1959, 1964) reported on the anopluran parasites of rodents, including sciurids, in Thailand, peninsular Malaysia, and parts of Borneo. Except for a few descriptive papers (Ferris, 1919, 1923; Johnson, 1959, 1964; Kuhn and Ludwig, 1965; Durden, 1991a), little has previously been published on any Anoplura from sciurids that are native to the islands on the Sunda Shelf and those lying to the east. Nevertheless, progressively fewer genera and species of sciurid-infesting Anoplura evidently accompanied their hosts in their southeastern colonization of the Indomalayan region, Sulawesi, and the Philippines. An alternative scenario would be that some of these louse genera did initially accompany squirrels in their southeastern colonizations but that these lice were eventually lost from these hosts. We have no

TABLE 56
Summary of Ectoparasite Records for the Species of *Rubrisciurus*, *Hyosciurus*, and *Prosciurillus*
(All the lice are described in the present report; published sources for fleas, ticks, and mites are referenced in the ECTOPARASITES subheading in species accounts of the squirrels.)

Host species	Sucking lice (Anoplura: *Hoplopleura*)[a]	Fleas (Siphonaptera: Leptopsyllidae, Pygiopsyllidae, Ceratophyllidae)	Ticks (Acari: Ixodidae)[c]	Mites (Acari: Mesostigmata)
Rubrisciurus rubriventer	*H. rubrisciuri*	*Medwayella rubrisciurae*[b], *Macrostylophora theresae*?	*Amblyomma* sp., *Dermacentor* sp., *Haemaphysalis* sp., *Ixodes* sp.	Unidentified Laelapidae
Prosciurillus leucomus	*H. leucomus*	—	—	—
Prosciurillus alstoni	*H. alstoni*	—	—	—
Prosciurillus weberi	—	—	—	—
Prosciurillus topapuensis	*H. topapuensis*	*Sigmactenus sulawesiensis*, *Farhangia sedecimdentata*[b]	—	—
Prosciurillus rosenbergii	—	—	—	—
Prosciurillus murinus	*H. murinus*	*Farhangia quatturrdecimdentata*, *Farhangia celebensis*[b]	—	Unidentified Laelapidae
Prosciurillus abstrusus	*H. abstrusus*	—	—	Unidentified Laelapidae
Hyosciurus heinrichi	*H. heinrichi*	—	*Amblyomma* sp., *Haemaphysalis* sp.	—
Hyosciurus ileile	*H. ileile*	—	*Dermacentor* sp., *Haemaphysalis* sp.	Unidentified Laelapidae

[a]All the species of *Hoplopleura* parasitizing the Sulawesi squirrels are host-specific.

[b]Recorded only from the squirrel host. WhenMardon and Durden (2003:81) described *Farhangia sedecimdentata* and *F. quatturordecimdentata* they noted that the morphological contrasts between the two clearly indicated different species, but could not determine their relationship to the earlier described *F. celebensis* just based on the original description of that taxon (Ewing, 1924). Ewing's description was sketchy and the illustrated characters showed some similarities with those of at least one of the new species Mardon and Durden had diagnosed. But all three species of *Farhangia* parasitizing Sulawesi squirrels are distinctive in their morphologies. Durden carefully examined the holotype (and only known specimen) of *F. celebensis* at the USNM and can attest to its diagnostic traits, which are not shared with the other two species. So two distinct species of *Farhangia* parasitize *Prosciurillus murinus*, and a separate species of *Farhangia* is found on *Prosciurillus leucomus*.

[c]Larvae and/or nymphs of ticks collected from Sulawesi squirrels can currently be identified only to genus (Durden et al., 2008).

proof for either phenomenon but, because external factors such as ambient temperature, relative humidity and host habitat, would presumably have little effect on the survival of permanent ectoparasites like sucking lice, we cannot speculate why lice would be lost from a particular host based on these factors alone. The diminution across China to the Sunda Shelf from seven genera of sucking lice to just one (*Hoplopleura*) on Sulawesi roughly parallels the decrease in squirrel taxa, from 22 genera (including flying squirrels) in three subfamilies and four tribes to the three endemic Sulawesian genera contained in one subtribe.

Three sciurid-infesting anopluran genera that occur on mainland Southeast Asia apparently have not colonized any of the Sunda Islands, Sulawesi, or the Philippines. As outlined above, two of these genera, *Linognathoides* and *Paradoxophthirus*, are specific parasites of sciurid taxa that similarly have been unable to colonize these islands. However, the third louse genus, *Ato-*

pophthirus, parasitizes *Petaurista elegans* (Kim, 1977), a flying squirrel that also inhabits the Greater Sunda Islands (Corbet and Hill, 1992; Thorington and Hoffmann, 2005) but from which this louse has not been collected in these insular locations.

Except for Sumatra (a very poorly worked island for Anoplura), the sciurid-specific louse genus, *Enderleinellus*, successfully accompanied squirrel hosts as far east as Borneo and Java (Johnson, 1964). However, *Enderleinellus* is unknown from Philippine or Sulawesian squirrels and therefore appears to have either failed to accompany the nannosciurines in their eastern-most colonizations east of the Sunda Shelf or to have been lost from them if this louse genus did initially accompany squirrels onto these islands. This apparent absence of members of *Enderleinellus* could reflect undercollecting for Philippine squirrels, but our meticulous searches of numerous Sulawesian squirrel pelts during this study, make us confident that *Enderleinellus* does not parasitize native squirrels on that island.

Hoplopleura shows an intriguing geographical distribution on Indomalayan squirrels (table 55). Species of this louse genus parasitize squirrels on mainland Southeast Asia but are currently known only from Philippine (one undescribed species known to us) and Sulawesian (eight new species described in this paper) squirrels within the broader Indomalayan region. If the ancestral squirrels reached the Philippines and Sulawesi via the Greater Sunda Islands, as seems likely, species of *Hoplopleura* would also be expected to parasitize squirrels on Borneo and/or Java, the principal Sundaic islands from which the ancestral squirrels presumably invaded the Philippines and Sulawesi. It is possible that *Hoplopleura* became extinct on Bornean and/or Javanese nannosciurine squirrels (perhaps because of competition from other genera of sucking lice) but it seems more likely that squirrel-infesting species of *Hoplopleura* await discovery on one or both of these islands. The sucking louse fauna of Bornean rodents has been fairly well documented by Johnson (1964), but surprisingly (because of its large human population with the associated removal of pristine forest habitats) the sucking louse fauna of native Javanese mammals is poorly known.

Nevertheless, just one invasion of Sulawesi by a representative of *Hoplopleura* (or its immediate ancestor) could feasibly account for the present diversity of this louse genus on the Sulawesian squirrel fauna. Theoretically, an ancestral lineage of *Hoplopleura* could have accompanied an ancestral squirrel lineage in its colonization of Sulawesi and then phyletically tracked this lineage as it evolved and radiated into the currently recognized endemic squirrel species in *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*. This scenario is consistent with results of molecular analyses by Mercer and Roth (2003: 1570) who indicated "a single lineage of squirrels crossed Wallace's Line to give rise to the three genera ... and multiple species of squirrels on Sulawesi." That ancestor (along with its obligate *Hoplopleura*) may have dispersed across the Makassar Strait from the Sunda Shelf to Sulawesi sometime between 11.4 to 10.5 million years ago (Mercer and Roth, 2003: 1571). Because neither *Enderleinellus* nor *Neohaematopinus* apparently accompanied colonizing squirrels into Sulawesi, host tracking and co-speciation by *Hoplopleura* or its ancestor of different endemic Sulawesian Hyosciurina squirrels may have been easier to accomplish in the absence of potential competition from members of *Enderleinellus* and *Neohaematopinus*.

The anopluran *Neohaematopinus* accompanied the ancestral nannosciurines throughout their ramifications into the Indomalayan region except for Sulawesi and most of the Philippines (the single known species from Sumatra and the absence of known species from Java probably reflect undercollecting). Apparently, *Neohaematopinus* did not accompany the nannosciurines to Sulawesi or to the Philippines proper (the only Philippine records are from Palawan, an island that lies on the Sunda shelf and that is zoogeographically more closely allied to Borneo than to other Philippine islands [Heaney, 1986]).

Results from analyses of future collections of sucking lice from Indomalayan sciurids will be used to test and refine some of the hypotheses presented here.

In the previous sections, we document information covering aspects of Sulawesi's endemic species of squirrels and their *Hoplopleura* parasites. We use these data as a painter's tool, a brush to render on a broad canvas a picture of Sulawesi squirrel systematics and their louse associates that is different from the usual image derived from contents in current published archives. While our depiction is intellectually and visually satisfying in its informational substance and zoogeographic texture, the picture is incomplete. Gaps remain. Portions of the canvas are without paint, other parts are fuzzy: hues and tones are diluted, outlines and shapes are undefined. Some spots will remain empty because the forests and squirrels, the source of the paint, have disappeared. Still, a nearly complete rendering could be accomplished, and the possible sources of the pigments needed for a final version are itemized in the next segment.

FUTURE INQUIRIES

Our analyses of data derived from museum specimens have allowed us to define eight species of tree squirrels in *Rubrisciurus* and *Prosciurillus* and two species of ground squirrels in *Hyosciurus* that are endemic to mainland Sulawesi, its offshore islands, and the Sangihe Archipelago. All species are diurnal. They exhibit an impressive range in body size (table 3) along with color pattern of pelage. From ecological observations and trapping data for certain species on the Sulawesi mainland, we know of their attachment to tall old-growth forests. Some species occur only in lowland tropical evergreen rainforest habitats, others are restricted to montane formations, and a few range from lowlands to montane environments (table 4). Within any locality, each species can be found on well-drained forested ridges, in valleys, and forests bordering streams and rivers. *Rubrisciurus rubriventer* and *Prosciurillus murinus* occur throughout most of Sulawesi, other species of *Prosciurillus* have restricted ranges on the mainland, and *P. rosenbergii* is the only squirrel known from islands in the Sangihe Archipelago (tables 3, 4). On the mainland, several species may occur in the same forest, but other distributions form parapatric or allopatric patterns (table 6). Understory habitats are occupied by *Rubrisciurus rubriventer* and *Prosciurillus murinus* (and probably *P. abstrusus*), the high canopy layer and emergent crowns are the foraging and nesting sites of members in the *Prosciurillus leucomus* group of species, and the two species of *Hyosciurus* are terrestrial. Fruits, seeds, and arthropods comprise the diets of those species for which this information is available (table 57). One or two young comprise the litters; *Rubrisciurus* has two pairs of teats, species in the other genera have three pairs (table 58).

Of the 10 species of squirrels, eight is each a host to a unique species of sucking lice in *Hoplopleura*. The lice comprise a monophyletic group relative to species of *Hoplopleura* parasitizing non-Sulawesi Indomalayan squirrels and endemic Sulawesi murid rodents (fig. 59). Their unique lineage mirrors that of the three genera of squirrels, which are monophyletic relative to other Indomalayan genera in the Nannosciurinae, one of the three subfamilies constituting Sciuridae.

Our portrayal of the endemic Sulawesi squirrels and their lice parasites should be viewed as a beginning, a first attempt towards understanding the actual regional and altitudinal distributions of the species, their ecologies, and their parasites. The results outlined here provide hypotheses that can be tested by analyses of data gathered in future inquiries. Researchers need to draw information from new biological surveys in particular regions of Sulawesi and employ not only the kinds of data analyzed here but additional sources of information, particularly that derived from focused observation of squirrel activities, and that obtained from genetic samples. In the following paragraphs we elaborate on the subjects that need to be addressed by fresh research efforts.

The Squirrels

***Prosciurillus leucomus*:** The northern peninsula of Sulawesi is the range we describe for *Prosciurillus leucomus*. It is drawn from suitably large samples collected on the northeastern end but fewer and smaller series from elsewhere on the peninsula. Size of nape patches and their contrast with the back-

TABLE 57
Summary of Fruit, Seeds, and Arthropods Eaten by Species of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*[a]

Species	Fruit and seeds	Insects and other arthropods
TREE SQUIRRELS (*Rubrisciurus*, *Prosciurillus*)		
R. rubriventer	*Ficus* spp. (figs), *Pangium edule*, (pangi), *Dillenia serrata* (dongi), *Elmerrillia ovalis* (uru), *Etlingera celebica* (ginger), *Pandanus* sp., *Rhaphidophora* sp. (moncot vine), other unidentified fruits and seeds.	**Insects in decaying wood:** beetle (Coleoptera) larvae without legs; adult beetles; termites (Rhinotermitidae), workers and soldiers; carpenter ant pupae and occasional adult ants. **Insects from other places**: buprestid beetle larvae (beneath rotting bark on rotting wood lying on ground or tree trunks), margarodid scale insects, Coccoidea (on tree trunks and low limbs); macrolepidopteran caterpillars (on leaves in understory or on ground leaf litter)
P. leucomus	?	?
P. alstoni	*Ficus* spp. (figs) and a variety of other soft fruits.	**Arboreal insects**: buprestid beetle larvae; several other kinds of beetle larvae; adult beetles; termites (Termitidae), workers and soldiers; macrolepidopteran caterpillars; the occasional ant, and ant pupae.
P. weberi	?	?
P. topapuensis	*Ficus* spp. (figs) and a variety of other soft fruits, a few kinds of seeds.	**Arboreal insects**: macrolepidopteran caterpillars; cockroaches; small larval and adult beetles.
P. rosenbergii	?	?
P. murinus	*Ficus* spp. (figs) and a variety of other soft fruits.	**Arboreal insects**: buprestid beetle larvae; other kinds of small beetle larvae; adult beetles; termites (Termitidae), workers and soldiers; macrolepidopteran caterpillars, inch-worm caterpillars (Geometridae); margarodid scale insects (Coccoidea); cockroaches. **Terrestrial insects**: cranefly larvae (Tipulidae); adult beetles; cockroaches.
P. abstrusus	?	?
GROUND SQUIRRELS (*Hyosciurus*)		
H. heinrichi	Primarily *Lithocarpus* spp. (acorns), a little soft fruit (unidentified).	**Terrestrial leaf litter arthropods**: Geophilomorph and Scolopendromorph centipedes; the occasional ponerine and formicine ants and ant pupae; long-legged, cursorial beetle larvae; several other kinds of beetle larvae with short legs; adult beetles; and cockroaches. **Subsurface insects**: Sciaroidea dipteran larvae; other kinds of dipteran larvae.
H. ileile	Primarily *Lithocarpus* spp. (acorns) and *Ficus* (figs); other kinds of fruit (unidentified), several kinds of large seeds.	**Terrestrial leaf litter arthropods:** pill bugs (Crustacea, Isopoda); Geophilomorph and Scolopendromorph centipedes; scorpions; orthopterans; occasional ants and ant pupae; adult beetles; long-legged, cursorial beetle larvae.

[a]The tropical Indomalayan nannosciurine tree squirrel *Sundasciurus hippurus* and ground squirrels *Rhinosciurus laticaudatus* and *Dremomys everetti* include earthworms in their diets (Davis, 1962; Payne et al., 1985); no remains of earthworms were found in stomachs of *Rubrisciurus rubriventer*, either species of *Hyosciurus*, or any of the species of *Prosciurillus* that Musser collected.

TABLE 58
Summary of Reproductive Information for Species of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*

Species of *Rubrisciurus*, *Prosciurillus*, and *Hyosciurus*	Number of teats	Litter size (evidence)
R. rubrisciurus	4 (2 inguinal pairs)	1 (embryo)
P. leucomus	6 (1 postaxillary, 2 inguinal pairs)	?
P. alstoni	6 (1 postaxillary, 2 inguinal pairs)	1 (embryo)
P. weberi	6 (1 postaxillary, 2 inguinal pairs)	?
P. topapuensis	6 (1 postaxillary, 2 inguinal pairs)	1 (placental scar)
P. rosenbergii	6 (1 postaxillary, 2 inguinal pairs)	?
P. murinus	6 (1 postaxillary, 2 inguinal pairs)	1 (embryo)
P. abstrusus	6 (1 postaxillary, 2 inguinal pairs)	?
H. heinrichi	6 (1 abdominal, 2 inguinal pairs)	1–2 (placental scars)
H. ileile	6 (1 abdominal, 2 inguinal pairs)	2 (embryos)

ground fur, along with coloration of fur covering underparts of head and body, vary noticeably among present samples, but not cranial and dental dimensions. East of the Gorontalo region the squirrels have bright, white, and expansive nape patches, and rich reddish orange underparts; west of Gorontalo the specimens examined exhibit the range from necks with large and conspicuous patches to diluted markings or none at all, and the underparts range from deep reddish orange to buffy orange. Female lice gathered from one specimen in the northeast and from one at the base of the northern peninsula in the west show slight differences in lengths of apical setae on some of the paratergal plates, but we consider this minor variation to be within the morphological limits of a single louse species because morphology of the subgenital plate and its associated setae of the lice from both squirrel specimens are highly distinctive compared with the morphologies found in the other Sulawesi species of squirrels. For the squirrels, the evidence from nape markings and color saturation of the underparts suggests some past, likely partial, suppression of gene flow between eastern and western populations, a pattern seen in macaques (Fooden, 1969) and some murid rodents (Musser's research). But more and larger samples of squirrels and their lice parasites are required from that region extending from the Gorontalo area west to the base of the peninsula so the variation in pelage coloration and patterning can be more completely described and its significance understood.

Prosciurillus rosenbergii: Specimens collected in the late 1800s and now stored in museums remain the only source of information about *Prosciurillus rosenbergii* in the Sangihe Archipelago. We know nothing of its altitudinal distributions on the various islands or anything about its ecology. We assume it is a species frequenting the upper canopy, as Musser observed for mainland *P. topapuensis* and *P. alstoni*, but because *P. rosenbergii* is the only squirrel on the four islands in Kepulauan Sangihe, it may be active at all levels of the forest, from the ground to the upper canopy layer. We need new inventories of indigenous mammals inhabiting the Sangihe islands, especially those living on Pulau Sangihe itself. If intact primary forest is still present, the squirrels should also be there; unfortunately, most of the original forests on Pulau Sangihe were long ago converted to plantations of coconut and nutmeg, and by 1920 most of the northern islands had lost their original forest cover (see the account of *P. rosenbergii*).

The specimens stored in museums consist of skins, some accompanied by damaged skulls. We could not assess variation among insular populations using data from cranial and dental measurements. This obstacle could be overcome by sampling hairs or sections of skins from the old specimens from which DNA might be extracted and gene sequences subsequently analyzed. The results would provide a picture of genetic variation among the island populations, at least among the populations that were present at the times of collection, and perhaps inform us about

degree of genetic isolation among the populations of squirrels from each island.

Prosciurillus weberi: A similar level of ignorance attends *Prosciurillus weberi*. We know of only eight specimens representing this species, all collected between 1889 and 1940 from the environs of Masamba and Palopo in the southern part of Sulawesi's central core. We strongly suspect that the actual range of *P. weberi* is more extensive than is indicated by the small sample stored in museum collections, possibly extending throughout the lowlands at the southern end of the western mountain block, south into the southwestern peninsula, and north along the western coastal lowlands of Sulawesi's central core (see the account of *P. weberi*). Its ecology is likely similar to that of *P. alstoni*, which occurs to the east of *P. weberi*'s range, but this is a guess in the absence of data. Future research should endeavor to illuminate the actual range of *P. weberi* as well as its ecological characteristics.

Allopatry among species in the *Prosciurillus leucomus* group: On mainland Sulawesi, *P. leucomus*, *P. alstoni*, *P. weberi*, and *P. topapuensis* have allopatric ranges relative to each other (see the map in figure 11). In the accounts of species we described the closest distances between collection localities for different sets of species'. Areas in between these ranges have yet to be sampled and we remain ignorant of the finer distributional relationships among the different species we have defined here, and their possible genetic interactions. Is there narrow sympatry along edges of the geographic ranges or does each abut in some parapatric pattern? Does each species retain its phenetic and genetic integrity at the range boundaries or is there gene exchange and some level of hybridization as has been documented among some of the very morphologically distinct species of Sulawesi macaques (Watanabe and Matsumara, 1991; Watanabe et al., 1991a, 1991b; Froehlich and Supriatna, 1996; Bynum et al., 1997; Groves, 2001; Evans et al., 2001, 2003)?

Rising and falling sea levels accompanied by tectonic uplift and subsidence, along with volcanism, have shaped Sulawesi through the Pleistocene, fragmenting it into an archipelago, and later reuniting the islands into a solid landmass (Fooden, 1969). Such past geological transformations are reflected in the present distributions of some animals endemic to Sulawesi's forests. In this context, the six (or seven, depending on the researcher) species of Sulawesi macaques are iconic, their species' formations tied to population isolation and genetic uniqueness on Archipelago Sulawesi with renewed population contacts after the island's restoration to a single body of land (Fooden, 1969). Sulawesi macaques have been the focus of intense observational, behavioral, morphometric and morphological, developmental, endoparasitic, and genetic inquiries (Albrecht, 1978; Watanabe and Matsumura, 1991; Watanabe et al., 1991a, 1991b; Suryobroto, 1992; Muroyama and Thierry, 1998; Gotoh et al., 2001; Groves, 1980b, 2001; see also the references in Evans et al., 2003). Distinct populations of the toad *Bufo celebensis* show geographic distributions concordant with those of *Macaca* (Evans et al., 2003). The ranges we sketch here for mainland members of the *Prosciurillus leucomus* group of species provide another potential set of distributional patterns that can be compared with those of macaques and toads. But to carefully test any congruence will first require collections of new material from regions of Sulawesi that are now unsampled for the *P. leucomus* assemblage of species, and from places between currently defined boundaries of each species.

Genetic relationships among species in the *Prosciurillus leucomus* group: We cannot currently describe the pattern of phylogenetic affinities among the species. We considered a cladistic analysis employing cranial and dental traits but rejected this approach as likely unproductive because the species are so similar except for color patterns of the fur and geographic distributions. Speculating about the degree of genetic relationship based on the allopatric pattern of the species' ranges is frustrating and could be misleading. For example, it seems reasonable to assume that *P. rosenbergii* in the Sangihe Archipelago would be more closely related to *P. leucomus* on the northern peninsula of Sulawesi, but the former is strikingly different in fur coloration from the latter, and from the other mainland species in the *P. leucomus* cluster. It is not far-fetched to look

on *P. rosenbergii* as an early offshoot from the ancestor of the group, and not especially closely related to any particular species.

Prosciurillus topapuensis is known only from the west-central region of Sulawesi's central core. In its range and color pattern, the species seems as isolated from surrounding species as is *P. rosenbergii* in the northern archipelago. *Prosciurillus topapuensis* does exhibit black ear tufts, which is characteristic of *P. leucomus* to the north and *P. weberi* to the southeast, and its altitudinal range embraces tropical lowland evergreen and montane rain-forest habitats, as does *P. leucomus*; by contrast, *P. weberi* and the eastern *P. alstoni* have been collected only in lowland forests. Do these observations have significance in unraveling the degree of phylogenetic affinity between *P. topapuensis* and any of the other species? Viewing another trait, *P. leucomus*, *P. alstoni*, and *P. weberi* share brightly pigmented venters (red to orange hues). Does this similarity signify a closer relationship among those three species than to *P. topapuensis* with its dark gray underparts?

We believe that analysis of data from gene sequences would be the most productive approach to recover phylogenetic relationships among species in the *P. leucomus* group. Results from such an endeavor may also identify the oldest member of the group and possibly inform the timing and geographic sequence of past isolation events on the island.

The *Prosciurillus murinus* group: Uniting the small-bodied *P. murinus* with *P. abstrusus* in opposition to the larger-bodied species in the *P. leucomus* group conforms strictly to morphological criteria. *Prosciurillus abstrusus* is typically physically larger than *P. murinus* and the outer surfaces of its ears are covered with short, white fur; otherwise, the two species are closely similar in pelage coloration and cranial conformation. A patch of fur covering the medial surface of each ear that contrasts with the head and neck, and that may or may not form tufts, is typical of Sulawesi's tree squirrels *Rubrisciurus rubriventer* and most of the species in the *Prosciurillus leucomus* group but not *P. murinus*. It is possible that *P. abstrusus* is a closer genetic relative of *P. leucomus* and the other members in that group than of *P. murinus*. On the other hand, swatches of fur on the ears that contrast with the head may be primitive for Sulawesian tree squirrels, a trait simply lost in *P. murinus*. While we strongly advocate the hypothesis that *P. abstrusus* is a montane representative of *P. murinus* that is genetically and geographically isolated on Pegunungan Mekongga, this assessment should be tested by obtaining results from analyses of gene sequences.

Except that *P. abstrusus* was collected in montane forest habitats, other aspects of its ecology are unknown, as is its altitudinal distributional in relation to *P. murinus*. Do the species exhibit similar ecologies? Does *P. abstrusus* descend into the upper reaches of tropical lowland evergreen rain forest and *P. murinus* penetrate montane habitats or are their ranges parapatric with *P. abstrusus* restricted to montane forest and *P. murinus* to lowland forest habitats? A careful survey of these species along a transect from lowlands at the base of Pegunungan Mekongga onto the mountain range would answer the questions.

We have a reasonable sample of skins representing *P. murinus* from the southern highlands of the southwestern peninsula, but could not compare covariation in cranial and dental variables for these specimens with other geographic samples. The skulls are missing, damaged, or juvenile. Measurements of length of maxillary tooth row average slightly larger than is typical for samples from regions outside the southwestern peninsula, suggesting that peninsular squirrels may average larger in body size. Study of fresh, intact specimens would help resolve the morphometric relationship between the peninsular population and those to the north.

Hyosciurus: We document the boundaries of two species of ground squirrels here, but our samples of the lowland form, *Hyosciurus ileile*, are small and from only one place on the northern peninsula and two areas in the northern part of the central core (see fig. 35). The actual geographic distribution of this species is unknown, but we suspect its range to be much broader than is indicated by present samples. If Musser's experience with the species is usual, it is uncommon in lowland and middle-altitude habitats, at least

in central Sulawesi, and would require targeted surveys to determine the boundaries of its true distribution over the island.

Hyosciurus heinrichi, on the other hand, appears to be plentiful in its mossy forest environs. Voucher specimens reflect a distribution confined to the western mountain block of Sulawesi's central core, a range concordant with the tree squirrel *Prosciurillus topapuensis* along with shrews, tarsiers, and a cluster of murid rodents (table 25). However, surveys are needed in other mountainous regions of Sulawesi—those on the east-central peninsula, for example—before this highland region can be confidentally recognized as an endemic haven for *H. heinrichi*, as well as the other mammal species listed in table 25.

Ecology

Nests: Other than the anecdotal observations concerning nests recorded for *Rubrisciurus rubriventer*, we provide scanty information covering nest sites. Musser did not detect leaf nests in tree crowns during the time he worked in Sulawesi. He suspects that members of *Prosciurillus* use tree holes and spaces in the accumulated debris contained by emergent strangler figs as nesting sites. The two species of ground squirrels may utilize burrows but may also construct nests inside decaying tree trunks lying on the ground. Whether a particular nest site is used faithfully during the life of a squirrel or different sites are utilized depending upon food availability, population density of predators, and season is unknown.

Diet: We provide dietary information for some species, but the survey of foods is incomplete. Not all the remains of fruits and seeds found in stomachs could be identified. Only segments of the year (or fruiting cycles, which may be less or more than 12 months in the tropics) are represented in our data (table 57). Dietary components need to be studied over a period that includes fruiting cycles (and their overlap or congruence among tree species) and seasonal fluctuations (rainy versus dry seasons). The foods we report here for a particular species collected during particular time segments may change over a longer period. For example, the montane ground squirrel *Hyosciurus heinrichi* consumes acorns and arthropods. Production of *Lithocarpus* may be high some years but low during others. During times of low yield does the squirrel consume primarily arthropods or does it turn to other kinds of fruit to supplement its diet? This is but one of the questions to be answered in any future study of Sulawesi's squirrels that focuses on diet.

Reproductive biology: Present reproductive information is meager. We can suggest litter size for the species collected by Musser (based on embryos and placental scars), but not for the others (table 58). Other questions require answers: How many litters are produced during a reproductive season? Is litter size fixed within a particular species of squirrel or does it change throughout the reproductive season depending on availability of food and nesting sites? These and other questions could be answered by comprehensive ecological studies of the different squirrel species endemic to Sulawesi.

Geographic Regions

The west-central region or western mountain block in Sulawesi's central core: This is the landscape of coastal lowlands, foothills, high peaks (some reaching 3000 m or more), and interior valleys latitudinally extending from the Palu area in the north (about 00°53′S) to the southern margin of Pegunungan Latimojong in the south (about 04°S), and longitudinally lying between the western margin of the island bordering the Makassar Strait and Danau Poso in the east (120°37′E). The mountains that form most of this region, the most extensive highland landscape on the island, are the product of Pliocene orogeny related to the late Miocene–early Pliocene collision of the Banggai-Sula Australian microcontinental fragment with eastern Sulawesi (Bergman et al., 1966; Wilson and Moss, 1999; Charlton, 2000; Calvert and Hall, 2006). Prior to this orogenic period "throughout the Early Miocene and, in places, until the Middle or Late Miocene, carbonates and mudstones were deposited on a shallow-marine continental margin" in western Sulawesi (Calvert and Hall, 2006: 366), and until the Pliocene western Sulawesi

may have "been little more than islands" (Hall, 2001: 49).

Throughout this western mountain block our attention focuses on uplands above 100 m where a suite of mammals have been collected only from this region. Three species of shrews (*Crocidura*), at least two and possibly three tarsiers (*Tarsius*), a tree squirrel (*Prosciurillus topapuensis*), one ground squirrel (*Hyosciurus heinrichi*), and 14 species of murid rodents mark the western highland complex as a center of mammalian endemism. A few species are found in tropical lowland evergreen rain forests covering lower altitudes on foothills and interior valleys, but most occur at higher altitudes in montane forests (table 25).

Turning to the squirrels, we have at hand samples of *Prosciurillus topapuensis* and *Hyosciurus heinrichi* from a very few places in this western mountain block, not enough samples to reliably discern geographic patterns of population variations and their significance (see accounts of the two species). New material from unsampled montane localities from throughout the highlands would be welcome, especially samples from which molecular data can be extracted to better determine the extent of genetic continuity or discontinuity among populations.

Approximately 350 m is the lowest record for *Prosciurillus topapuensis* along Musser's transect in the Danau Lindu area. The lowest altitudinal limit for the species throughout the rest of the west-central region is unknown. The few other samples are from montane forests. How low does *P. topapuensis* descend along the margins of the mountain block adjacent to the distributions of the lowland *P. alstoni* and *P. weberi*? Does *P. topapuensis* inhabit the coastal forests 100 m and below along the fringe of the Makassar Strait or is it excluded by a different species in the *P. leucomus* group (see above)?

Except for the Danau Lindu area and adjacent mountains, the altitudinal distributional pattern of *Hyosciurus heinrichi* and *H. ileile* is unknown throughout most of the western mountain block. Does *H. ileile* occur throughout lower altitudes in the region in a parapatric pattern similar to that present on Gunung Kanino, or is it absent from some places where the lower altitudes are occupied by *H. heinrichi*?

The eastern central core and east-central peninsula: The distribution of squirrels in the eastern portion of Sulawesi's central core and the east-central peninsula is currently a mystery. We suspect that surveys throughout that region would document the presence of *Rubrisciurus rubriventer* and *Prosciurillus murinus*, for these two species are recorded from the western part of the central core and the other arms of Sulawesi (see the distribution maps in figures 5 and 30). The type series of *tonkeanus* is the only sample of *Prosciurillus alstoni* we know about from the east-central peninsula, but the species probably ranges throughout the region in tropical lowland evergreen rain forest. If it does, we need to know the extent of geographic variation in expression and color of ear tufts along with other pelage traits.

Hyosciurus ileile, the lowland ground squirrel, may also be encountered in the east-central peninsula but the montane *H. heinrichi* of the western mountain block in the central core may not. Very little is known about the montane rodent fauna in the east-central arm of Sulawesi. To date, the only highland area sampled for small mammals is Gunung Tambusisi (01°38′S, 121°23′E) near the western end of the peninsula. Two rats, *Bunomys prolatus* and *Maxomys wattsi*, are recorded from montane habitats on the mountain (Musser, 1991). Neither species occurs on any other sampled mountain range elsewhere on Sulawesi, suggesting that the east-central peninsular mountains may harbor a unique assemblage of rodent species (and possibly representatives of other mammalian orders) restricted to mossy forest environments. That group may contain distinct species of squirrels, possibly a species of *Hyosciurus*, with traits different from those characterizing *H. heinrichi*. If *H. heinrichi* or a close montane relative does not occur in those peninsular highlands, possibly the montane forests are occupied by *H. ileile* ranging up from the lowlands.

A member of the *Prosciurillus leucomus* group, other than *P. alstoni*, might also occur in the uplands of the east-central peninsula. Outside Gunung Tambusisi, the places to expect endemic montane squirrel species

would be in the other highland regions of the east-central arm: Gunung Tokala to the east of Gunung Tambusisi, Gunung Katopasa to the north, and Gunung Bulutumpu farther out on the peninsula (see the map in Whitten et al., 1987: 498). Pegunungan Pompangeo to the west of Gunung Tokala and northeast of Danau Poso is another potential montane region that should be surveyed to determine if a montane member of the *P. leucomus* cluster occurs there, and if *H. heinrichi* or another kind of ground squirrel is also present. These mountains and stretches of highlands connecting them are isolated from the western mountain block in the central core of the island.

The contention that the east-central peninsula is home to a species of macaque distinct from *M. tonkeana* (Froehlich et al., 1998), the species found in central Sulawesi, is another indication of the possible surprises awaiting future surveyors of the east-central arm.

Results of surveys for small mammals in the east-central peninsula will also be important for testing the endemic stature of the west-central region. Currently, 23 species of small mammals have been found in the western mountain block and nowhere else on Sulawesi (see above). Finding none, or only a few of these species in the east-central peninsula would certainly strengthen the position of the west-central region as an area of significant endemism in the evolutionary history of Sulawesi's mammals.

Southeastern peninsular islands: Kabaena, Muna, and Buton, three large islands off the southern coast of the southeastern peninsula, have been inadequately surveyed for their squirrel populations. We examined two old specimens said to come from Buton. Characteristics of their skulls and fur coloration and patterning closely resemble our samples of *Prosciurillus alstoni* from the mainland (see that account). The population on Pulau Kabaena is represented by only Schwarz's (1911) published description of "*Sciurus elbertae*" and two skulls, a very young adult and a juvenile (see the account of *P. alstoni*). Although we ally the Buton and Kabaena samples with mainland *P. alstoni*, this postulated kinship needs to be tested by study of fresh and larger samples. We have not seen any squirrels from Pulau Muna. *Rubrisciurus rubriventer* and *Prosciurillus murinus*, which inhabit mainland lowland forests, should also occur on each of the three islands; if so, they have yet to be collected there.

Western coastal lowlands of the central core: The coastal lowlands fringing the western margins of the western mountain block in Sulawesi's central core, from the Palu area south to the northern sector of the southwestern peninsula, is another area that requires biological surveys for small mammals. The tree squirrels *Rubrisciurus rubriventer* and *Prosciurillus murinus* should be expected there, but we are uncertain which species in the *Prosciurillus leucomus* group would be encountered. *Prosciurillus weberi* is currently represented by a few specimens collected from a small area in the southern part of the central core of Sulawesi (see the map in figure 11) and may range north along the western coastal lowland forests. On the other hand, *P. topapuensis*, endemic to the western mountain block, may extend into low altitudes and occupy forests all along the coast (see those species' accounts).

Genetic Analyses

Genetic analyses: New samples of all 10 of the species of squirrels we document here should include tissues from which DNA can be extracted. Results from phylogenetic analyses of gene sequences could be used to test the following. **(1)** Whether geographic samples of *Rubrisciurus rubriventer* and *Prosciurillus murinus* represent single species that range throughout most of Sulawesi. **(2)** The genetic integrity of the five species we define in the *Prosciurillus leucomus* group, the presence or absence of hybridization along their range borders, and phylogenetic affinities among them. **(3)** Whether a single species is represented by current samples we define as *P. leucomus* from the northern peninsula, with east-west geographic variation in pelage traits. **(4)** The pattern of genetic variation among insular populations of *P. rosenbergii* in Kepulauan Sangihe. **(5)** The supposition that voucher specimens of *Hyosciurus ileile* from the northern peninsula and central core are drawn from populations representing the same species, but one exhibiting geographic variation possibly concordant with distribu-

tions on the northern peninsula and central core. **(6)** Whether our samples of *H. heinrichi* represent a single species that exhibits morphometric variation in cranial and dental traits among montane populations.

Fresh samples of squirrels may not be necessary for analyses of gene sequences. We have identified voucher specimens by catalog numbers and the institutions where they are stored. Hairs or bits of dry tissue from those specimens might yield viable DNA to be employed in analyses to substantiate or modify our template of species-diversity.

The Lice

Sucking lice (*Hoplopleura*): Samples of two of the Sulawesi tree squirrels, *Prosciurillus weberi* and *P. rosenbergii*, did not yield sucking lice in our survey. Fresh specimens of these two species are needed to determine if each supports its own distinctive species of louse, which would fit with the pattern of host-parasite relationship characterizing the other eight endemic species of Sulawesi squirrels. Two other squirrel hosts, *P. leucomus* and *P. alstoni*, did yield samples of *Hoplopleura*, and while they were sufficient to indicate that each represents a separate species unique to their hosts, the samples contained only females and nymphs. Because male lice were absent from these samples, their morphological traits could not be incorporated into our phylogenetic analyses of Sulawesi *Hoplopleura*. Additional samples containing male lice will be required to augment descriptions of the two species, and to provide characters needed to determine if they are part of the monophyletic clade containing the other species of lice parasitizing the endemic squirrels.

Just as the diversity of squirrel species we describe here requires testing using molecular data, so does our interpretation of anatomical differences among samples of sucking lice. Analyses of mitochrondrial and nuclear gene sequences would provide insight into the accuracy of species-diversity documented here as well as the pattern of phylogenetic relationships of the lice recovered from our cladistic analysis based on external anatomy. Some Sulawesian squirrel study skins in various museums undoubtedly still have (desiccated) louse specimens attached to them; these louse specimens could be rehydrated and, in some cases with the appropriate techniques, viable DNA may still be harvested from them.

Forest Cover

We are not unaware that the future surveys we suggest may be impossible to implement because of past forest destruction and continuing transformation of primary forests into anthropogenic landscapes in some regions of Sulawesi. Opportunity to learn about the squirrel fauna in the southern portion of the southwestern peninsular lowlands, for example, disappeared long ago with the conversion of primary habitats to agricultural crops. Skeletal fragments from archaeological surveys constitute the primary evidence for the composition of species that once occurred there. However, intact forests remain elsewhere on the island, even outside of protected natural reserves and national parks (see the map in Supriatna et al., 1992: y37; and map 8d in MacKinnon, 1997).

EPILOGUE

By about 10 million years ago, "The Makassar Strait was still fairly wide but there is at that time the first good evidence for the emergence of land in much of Sulawesi" (Hall, 2001: 52; also see Calvert and Hall, 2006), "although west Sulawesi may itself have been little more than islands until the Pliocene" (Hall, 2001: 49). Between 11.4 and 10.5 million years ago a single ancestral squirrel lineage, likely accompanied by its unique species of sucking louse, crossed the Makassar Strait from the Sunda Shelf to this early Sulawesi Archipelago; from it evolved eight species of tree squirrels and two species of ground squirrels in three monophyletic clusters (genera) that now reside on the island and nowhere else. Habitats in the forest understory are occupied by the largest of the endemic squirrels, *Rubrisciurus rubriventer*, and the smallest, *Prosciurillus murinus*. Five species of *Prosciurillus* live in the upper forest tree canopy, and two species of *Hyosciurus* are terrestrial, inhabiting lowland and montane forests. The

extant products of this radiation, although unique to Sulawesi, comprise a range of physical size and general ecology similar to that seen in parts of the nannosciurine squirrel fauna inhabiting the forests of Borneo, across the Makassar Strait west of Sulawesi.

The Sulawesi red squirrel is the largest of the island's endemic suite. It has no actual counterpart on Borneo, but its occurrence in the forest understory and on the ground, along with a diet of fruit, seeds, and insects, recalls the Bornean population of *Sundasciurus hippurus*. Although physically smaller than *Rubrisciurus* (260–365 g versus 500–860 g), the general conformation of its skull resembles that of *Rubrisciurus*, including procumbent incisors. *Sundasciurus hippurus* is active in the understory where on Borneo it is "Most often seen in small trees but sometimes travels on the ground" (Payne et al., 1985: 239), and on the Malay Peninsula the squirrel is "Largely restricted to tall forest, ranging from the under-canopy to the ground" (Medway, 1969: 59). Diet consists of pulpy fruit, seeds, earthworms, and insects (Davis, 1962: 79; Payne et al., 1985: 239).

Rheithrosciurus macrotis, a Bornean endemic, and one of the giants of the species in the squirrel fauna recorded from that island (1170–1280 g), is also found mostly on the ground or low on tree trunks, but is strikingly different from *Rubrisciurus* in color pattern of the fur and cranial morphology (see the description of *R. macrotis* in Payne et al., 1985: 243; see Moore, 1959, for cranial traits), and a member of a different evolutionary lineage (Sciurinae rather than Nannosciurinae; see Mercer and Roth, 2003, and our classification section).

The two species in the *Prosciurillus murinus* group, *P. murinus* and *P. abstrusus*, are the smallest in body size among Sulawesi's indigenous squirrels (length of head and body = 102–150 mm). Their physical stature and vertical distribution in the forests (at least for *P. murinus* for which there are ecological data) are comparable to the Bornean populations of *Callosciurus adamsi* and *C. orestes*, along with *Sundasciurus lowii* and *S. tenuis* (collective lengths of head and body = 131–183 mm); all are small-bodied, subcanopy species and include fruits, seeds, and arthropods in their diets (Davis, 1962: 81; Payne et al., 1985).

Prosciurillus leucomus and its allies in the *P. leucomus* group inhabit the upper levels of primary forest on mainland Sulawesi; their canopy counterpart on Borneo is *Callosciurus prevostii*, although it is larger in body size than the Sulawesi species (250–500 g versus 135–210 g); *C. prevostii* consumes a variety of soft fruits along with insects, dietary components similar to those species in the *P. leucomus* group (see Davis, 1962, and Payne et al., 1985, for accounts of Bornean populations).

The two species of Sulawesi ground squirrels recall two species in two genera living on Borneo. *Hyosciurus heinrichi* is reminiscent of Borneo's population of the shrew-faced ground squirrel *Rhinosciurus laticaudatus*. Both have very long muzzles and are about the same body size (length of head and body = 195–233 mm for *R. laticaudatus* [Payne et al., 1985: 242], 195–240 mm for *H. heinrichi*). Both species eat insects, but *H. heinrichi* includes *Lithocarpus* and other fruits in its diet while *R. laticaudatus* is more specialized, feeding exclusively on insects and earthworms (Davis, 1962: 81; Medway, 1969: 62). *Hyosciurus ileile*, with a shorter muzzle, is physically much larger than the Bornean endemic ground squirrel *Dremomys everetti* (293–520 g versus 75–185 g), but resembles that species in general conformation of the skull (see Moore and Tate, 1965: 261, for a drawing of the skull of the Chinese long-nosed ground squirrel *Dremomys pernyi*, which has a cranial conformation closely similar to that of the Bornean *D. everetti*); both consume fruit and insects (*D. everetti* also eats earthworms; Payne et al., 1985: 242).

Three groups of squirrels found on Borneo have no counterparts on Sulawesi. The giant squirrel *Ratufa affinis* (875–1500 g) is a member of one of the the oldest of the phylogenetic lineages within the Sciuridae (Mercer and Roth, 2003; Steppan et al., 2004). On Borneo, *R. affinis* lives in tall forest, coming to the ground only to cross gaps in the forest canopy (Payne et al., 1985: 233). Species of pygmy squirrels in *Nannosciurus* (length of head and body = 62–82 mm)

Fig. 60. Valley of Danau Lindu, 1000 m, in the northern highlands of the western mountain block of Sulawesi's central core. Part of Tomado village is in the foreground on the shore of a small cove. Tropical lowland evergreen rain forest is at lake level and mantles hillsides of the closer ridges. Upper slopes and summits in the background are clothed in montane forest formations. The large, red tree squirrel *Rubrisciurus rubriventer* lives in intact forest near the lake and in forests on the ridges to about 1500 m. Montane forests on the upper slopes and summits of the higher ridges (Gunung Nokilalaki is the farthest ridge seen in the background), support one ground squirrel, *Hyosciurus heinrichi*, which abuts the range of the other ground squirrel *H. ileile* at 1400–1500 m, and that species, while uncommon, occurs throughout the region at lower altitudes. The tree squirrels *Prosciurillus topapuensis* and *P. murinus* inhabit all old-growth habitats, from lakeside to tops of the highest ridges. Photographed in 1976.

and *Exilisciurus* (length of head and body = 62–93 mm) are the smallest in body size of the nonvolant Bornean squirrels; nothing like them is part of the modern squirrel fauna on Sulawesi. Finally, 8 genera and 14 species of flying squirrels inhabit Bornean forests (Payne et al., 1985); if an ancient ancestral flying squirrel lineage crossed from the Sunda Shelf to the early Sulawesi archipelago, it is not represented in Sulawesi's modern cluster of endemic sciurids.

The suite of squirrel species is just one component of the unique modern assemblage of native mammals living in the old-growth forested landscapes of Sulawesi and its nearby islands. They are joined by phalangers (two genera and at least five species), shrews (nine species of *Crocidura*), several species of bats and tarsiers, macaques (six or seven species of *Macaca*), rats and mice (at least 46 species in *Crunomys*, *Echiothrix*, *Tateomys*, *Melasmothrix*, *Sommeromys*, *Margaretamys*, *Lenomys*, *Eropeplus*, *Haeromys*, *Maxomys*, *Bunomys*, *Paruromys*, *Taeromys*, and *Rattus*), anoas (two species), pigs (*Sus celebensis* and one or more species of *Babyrousa*), and the top viverrid carnivore *Macrogalidia*. All are the modern products of a faunal evolution in isolation; ancestral lineages for some groups—squirrels, for example—likely date to late Miocene, at a time when the beginnings of Sulawesi likely existed as an

archipelago and was already separated from the Sunda Shelf margin by a deep strait.

The man thought about the island's unique mammals as he looked over the lake valley from his camp on a high ridge (fig. 60). Strident barking honks from three knobbed hornbills were answered by a squirrel's scolding chatter as all squabbled over ripe figs high in the crown of a strangler fig near his tent

Forests clothing the hills and mountains stepping away from lake-side to horizon had day by day and month by month yielded some of their secrets. He remembered an Indonesian saying: "*Ada udang dibelakang setiap batu*"; there is a crayfish behind every rock, meaning everything is not as it seems—what appears only as a rock in a stream is really the fortress of a crayfish. Across the horizon, there seemed to exist only undulating ridges of different heights mantled by tropical rain forest, but hidden beneath the canopy resides an assemblage of mammals unique to Sulawesi, and in the unseen rocky foundation beneath the forest floor is preserved a record of the island's tectonic origin.

A lone hornbill left the fig and flew high over the lake, its noisy barking honks and loud whooshing produced by the slow beating of its wings resonated in the tropical air. The bird was quietly replaced by a second squirrel arriving at the fig from an adjacent magnolia, its presence marked only by the arcing branch and rustle of leaves in the canopy.

Encountering the squirrels had been especially satisfying to the man: the chattering tree squirrels in the upper canopy; the aggressive little brown squirrels announcing their positions low on tree trunks; the silent, wary red squirrel bounding across leaf litter; and the elusive ground squirrels, glimpsed here and there as flashes of dark brown in the deep forest.

Thick gray clouds layered the valley, resting on dark green mountaintops as if anchored by the tops of trees emerging above the canopy. Earlier just a sigh through the crown of the strangler fig, the breeze turned into gusty wind, its intensity reflected in the clouds moving rapidly across the valley. The gray clouds were soon pushed to the horizon by low, black pillows portending rain. With the first few drops came calls from squirrels and forest birds announcing the impending downpour. Sound of hard rain on leaves quickly silenced squirrel chatter and birdsong. The remaining hornbills left the strangler fig, honking and barking across the valley as they whooshed through the dark and wet sky to disappear into the brooding gloom.

ACKNOWLEDGMENTS

An extraordinary group of talented persons unselfishly contributed their time and efforts to our project. Chris Smeenk (RMNH) searched through the collection at Leiden for all the type specimens of squirrels, provided measurements, and suggested which of those specimens should be recognized as holotypes, lectotypes, and paralectotypes. He also sent us invaluable information covering routes and travel dates of the collectors working in Sulawesi in the 1800s, sent us photocopies of pages from the classical Dutch natural history literature, translated original descriptions of squirrel taxa from Dutch to English, critically reviewed several of our long taxonomic and other sections, and shared with us accounts in his unpublished catalog of type specmens at Leiden. Clara Stefen (SNSD) checked all type specimens, supplied measurements, sent us color images of types, and scoured through the files at Dresden for answers to our queries. Earlier, Alfred Feiler (SNSD) had kindly loaned us samples of *Prosciurillus rosenbergii*. Paula Jenkins (BMNH) arranged for Sulawesi squirrel pelts to be examined for ectoparasites, measured type specimens as well as samples of *Prosciurillus topapuensis* and *Hyosciurus heinrichi* collected by W.J.C. Frost, searched through the literature to help us locate collection sites, and provided many other bits of useful information. Michael Carleton (USNM) arranged for Durden to survey study skins for ectoparasites and measure specimens, checked Musser's measurement values for some specimens, and illuminated some of the arcane (in Musser's view) procedures attending production of principle-components analysis. Loïc Costeur (NMB) measured types for us, sent color

images of all types, and provided other data about the collection of Sulawesi squirrels at Basel. Gerhard Storch (SMF) sent measurements for the holotype of "*Sciurus elbertae*" and supplied other relevant information. Pak Ucok Sinaga (MZB) provided measurements from the series of *Prosciurillus weberi* stored at MZB. Wim Bergmans (ZMA) sent us data from their collection of Sulawesi squirrels. Sujit Chakraborty verified the presence of the holotype of *alstoni* at the Zoological Survey of India and sent us measurements. Darrin Lunde (AMNH) provided us with copies of publications, answered queries about specimens, and provided constant and dependable help in other ways. David Grimaldi (AMNH) utilized his vast knowledge about insect diversity in helping us identify samples taken from stomachs of squirrels and gave to us insights covering habitats of these prey items. John Wahlert (AMNH) helped with the identification of certain cranial foramina. Ilkka A. Hanski (University of Helsinki, Finland) provided the study skin of a Sulawesi squirrel from which we first collected lice. Nancy E. Adams (deceased) (USNM) and Oliver S. Flint, Jr. (USNM) provided access to the USNM Collection of Anoplura. Christopher H.C. Lyal (BMNH) provided access to the BMNH Anoplura collections. Ta-Hsiung Chin (Giuyang Medical College, Guizhou Province, People's Republic of China) provided current information on, and specimens of, Chinese Anoplura.

Lance Durden's fieldwork in Sulawesi in 1985 was funded by a grant from the Committee for Research and Exploration of the National Geographic Society; he was sponsored in Indonesia by the Royal Entomological Society as part of "Project Wallace" (this report is "Results of Project Wallace no. 160") and by the Lembaga Ilmu Pengetahuan Indonesia (LIPI). Lance Durden and Jessica Light acknowledge an Anoplura grant received from the National Science Foundation (DEB-0717165). Guy Musser's fieldwork in Sulawesi was supported by the Celebes Fund of the AMNH as well as Archbold Expeditions, Inc.; he was sponsored in Indonesia by LIPI and the MZB. He was also assisted by members of United States Navy Medical Research Unit No. 2 (NAMRU-2) in Jakarta. Aileen H. Sherman and Donna Collins skillfully prepared drawings of some of the lice; the line drawings of squirrel skulls, and all distribution maps are the work of Patricia Wynne; photographic prints of habitats were produced by Peter Goldberg. We are grateful to all the curators and supporting staff of the various institutions we visited, and appreciatetheir willingness to provide access to specimens and other kinds of data. Margareta Becker, Aminudi, and Usma worked with Musser in Sulawesi—their efforts contributed significantly to results presented here. We applaud Nancy Simmons and the staff in Mammalogy at the American Museum of Natural History for their continuing support of Musser's research projects. And to the originator of the Celebes Fund: thank you once again. This report constitutes publication number 1217 of the Texas Cooperative Wildlife Collection and number 177 of the Center for Biosystematics and Biodiversity, both at Texas A&M University.

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APPENDIX 1.
Data Matrix for Species of *Hoplopleura* Parasitizing Sulawesi Squirrels and Murid Rodents
(*N* = not available)

Characters	1 2345678901	2 2345678901	3 2345678901	4 23456789012 3
Hoplopleura trispinosa	2000000111	1000011110	0111001000	0111100000
Hoplopleura distorta	2000110101	1100101101	01012N0100	0100111000
Hoplopleura erismata	1000110110	1100001111	1011000010	2000110111000
Hoplopleura thurmanae	1000010111	1101001111	1011000010	2000100101101
Hoplopleura abstrusus	1100110101	0110001111	001111N011	1011000100002
Hoplopleura heinrichi	1000000100	0111100111	0121000111	0010011100011
Hoplopleura ileile	1000000101	0110000111	0101111001	1110000001101012
Hoplopleura murinus	2100110101	0010101111	1112012N01	1110111011111012
Hoplopleura rubrisciuri	1000000001	0110000111	1001N12N01	1110000001100011
Hoplopleura topapuensis	1000010101	0110001111	1111111N01	1110101010110011
Hoplopleura chrysocomi	2000000101	1101001100	1012000010	2010111001101
Hoplopleura musseri	0000110131	0201001100	1112000110	3001001001000
Hoplopleura sembeli	1100000101	1111001100	1012000011	1011111000011
Hoplopleura traubi	1100111111	1201101100	1112000011	00N1101000010

APPENDIX 2

The Descriptions of *Sciurus rubriventer*, *Sciurus leucomus*, and *Sciurus murinus* by Müller and Schlegel (1844: 86–87) in the Original Dutch

"5.) **Sciurus rubriventer**, Forsten, n. sp. Grootte, vorm en kleur, het algemeen als van de voorgaande soort; maar de ooren grooter en veel sterker met zwarte haren bedekt, welke zeer lang zijn, en derhalve verre boven de ooren uitsteken. Het bruin-rood der onderdeelen strekt zich niet alleen over de binnenzijden, maar ook over de buitenzijden der pooten uit. Haren des staarts zwart, tegen de punten met breede, flaauw rood-bruine ringen. Celebes."

"9.) **Sciurus leucomus**, Forsten, n. sp. Grootte en vorm van de beide voorgaande. Ooren, van binnen met bruinachtig gele, van achteren met lange zwarte, verre boven de ooren uitstekende haren digt bezet. Kleur der bovendeelen en buitenzijden der pooten olijfbruin; de haren met roestgele ringen en gedeeltelijk met zwarte punten. Staart, met de genoemde drie kleuren geschakeerd. Eene groote witte vlek achter de ooren, aan weêrszijden van den hals. Onderdeelen van het ligchaam roestkleurig, in het rood-bruine trekkende. Celebes."

"11.) **Sciurus murinus**, Forsten, n. sp. Aanzien en vorm als van de voorgaande soort, maar een weinig kleiner; de staart eenigzins korter; de ooren minder behaard, en de kleur eenvormiger: van boven muisgraauw en de haren met witachtig gele punten; van onderen aschgraauw. Celebes."

APPENDIX 3

The Description of *Sciurus tonkeanus* by Meyer (1896: 25) in the Original German

"Sciurus tonkeanus n. sp.

Tafel X Figur 1 (c. ¾ n. Gr.)

Sciurus Sc. leucomo M. Schl. similis, sed minor, macula collari albescenti pilisque auricularibus nigris *nullis* et supra caudaque flavescentior (umbrino-flavo-ochraceus *Rdgw.* III, 17).

Hab. Tonkean, insulae Celebes peninsula septentrionali-orientalis.

Nom. Ind. *siling.*

Kleiner und farbiger als *Sciurus leucomus Müll. Schl.*, von der nördlichen Halbinsel des Landes, von wo die Art aus der Minahassa und dem Gorontaloschen bekannt ist (Jentink Cat. XII, 25 1888). Von *Sc. tonkeanus* liegen mir nur platte Felle ohne Knochen vor, so dass genaue Maasse nicht zu geben sind. Das fehlen der zwei hellen Halsflecke und der schwarzen Ohrbüschel, wie *Sc. leucomus* sie aufweist, unterscheidet *tonkeanus* leicht; an den Ohren ist ein Büschel nur angedeutet und hellbräunlich, wie die ganze Ohrberandung.

Aus der *Leucomus*-Gruppe sind nunmehr von Celebes drei, auch als Subspecies aufzufassende Formen bekannt:

leucomus Müll. Schl. von Nord Celebes,

weberi Jent. Von Central Celebes (Weber: Zool. Erg. I, 115 pl. VIII u. X, 1–3 1890–91) und

tonkeanus von Nordost Celebes,

die an ihren geographischen Berührungzonen vielleicht mehr oder weniger in einander übergehen. Vom Süden des Landes ist, meines Wissens, noch kein *Sciurus* der *Leucomus*-Gruppe registrirt; ob der hier vorkommende nun *Sc. weberi* oder eine vierte Subspecies sei, wird die Zukunft lehren.

Sc. weberi unterscheidet sich von *tonkeanus* durch einen schwarzen Rückenstreif und das Schwarz an den Ohren, sowie durch im Allgemeinen röthere Färbung."

APPENDIX 4

The Descriptions of *Sciurus sarasinorum* and *Sciurus leucomus occidentalis* by Meyer (1898: 1–3) in the Original German

"Sciurus sarasinorum n. sp.

Mas. *Sciurus Sc. leucomo Müll. Schl.* simillimus, sed penicillo auriculari albo maculaque collari albescenti nulla.

Hab.: Celebes centralis.

Die Art ist durch die (bei dem einen Exemplare bis zu 16 mm langen) ganz weissen Ohrbüschel, sowie durch das Fehlen des weisslichen Fleckes am Hinterhalse leicht von Sc. leucomus Müll. Schl. zu unterscheiden. Dr. P. und F. Sarasin erbeuteten auf ihren so erfolgreichen Reisen in Celebes zwei Männchen, und zwar das eine (Balg mit Schädel) in Ussu, Nordostecke des Bonigolfes (18, II 96), das andere (in Spiritus) in Mapane, Südufer des Tominigolfes (II 95), es ist also wahrscheinlich, dass dies die Central Celebes-Form der Leucomus-Gruppe ist. Das Exemplar von Mapane hat die weissen Ohrbüschel nicht so stark entwickelt wie das von Ussu und es bleibt daher noch offen, ob dies ein unterscheidender Charakter zwischen den Individuen aus dem Norden und dem Süden von Central Celebes ist. Das von Ussu hat ausserdem mehr schwarz und wenig Braun in den Haaren der Schwanzoberseite, so dass diese fast Schwarz und weiss geringelt ist. Nach einem Exemplar ist dieser Charakter nicht zu beurteilen, da die Schwanzfarbe von Sc. leucomus mehr oder weniger nach Alter, Geschlecht oder Jahreszeit variirt.

Sciurus weberi Jent. (Webers Zool. Erg. I, 115 tab. VIII u. X, 1–3 1890) stammt von nahe Palopo, das in der Nordwestecke des Bonigolfes liegt, und ist leicht durch den schwarzen Rückenstreif zu unterscheiden, es hat auch schwarze Ohrbüschel. Von einem der drei dort von Weber erbeuteten Exemplare sagt Jentink, dass die schwarzen Ohrpinsel leicht mit Weiss gespitzt seien, was mir insofern von Bedeutung scheint, als es einen Uebergang zur Central Celebes-Form, Sc. sarasinorum andeuten könnte. Bereits 1896 (Abh. Ber. 1896/7 Nr. 6 S. 25) besprach ich die Formen der Leucomus-Gruppe von Celebes und sagte: 'Aus dieser Gruppe sind nunmehr von Celebes drei, auch als Subspecies aufzufassende Formen bekannt:

leucomus Müll. Schl. von Nord Celebes,

weberi Jent. von Central Celebes und

tonkeanus A. B. M. von Nordost Celebes,

die an ihren geographischen Berührungszonen vielleicht mehr oder weniger in einander übergehen. Vom Süden des Landes ist, meines Wissens, noch kein Sciurus der Leucomus-Gruppe registrirt; ob der hier

vorkommende nun Sc. weberi oder eine vierte Subspecies sei, wird die Zukunft lehren.' Nunmehr scheint es, dass Sc. sarasinorum Central Celebes (und vielleicht Südost Celebes), weberi vielleicht Südwest Celebes oder den nördlichen Theil davon bewohnt, wenn im Süden und Südosten nicht noch andere Formen entdeckt werden sollten, was mich nicht überraschen würde. (Auf dem Pik von Bonthain ist ein Eichhörnchen gesehen worden, l. c.)."

"Sciurus leucomus occidentalis n. subsp.

Vor zwei Jahren (Abh. Ber. 1896/7 Nr. 6 S. 26) habe ich bereits hervorgehoben, dass die Leucomus-Exemplare aus dem Gorontaloschen den weisslichen Fleck am Hinterhalse wenig oder gar nicht entwickelt zu haben scheinen und gesagt: 'Sollte hier vielleicht eine Uebergangsform von der typischen weissfleckigen der Minahassa zu einer noch unbekannten ungefleckten südlicheren Form vorliegen, wie Sc. tonkeanus vom Nordosten, aber mit Schwarz an den Ohren? In der Berührungszone zweier solcher Subspecies dürfte der betreffende Charakter mehr oder weniger ausgeprägt sein.' Diese meine Vermuthung wird durch die Ausbeute der Herren Sarasin in folgender Weise unterstützt:

Fünf Exemplare aus der Minahassa zeigen den weisslichen Fleck am Hinterhalse gut ausgeprägt, und zwar:

1 mas (Balg mit Schädel) von Tomohon (III 94)
1 mas (in Spiritus) von Tomohon (III 94)
1 mas (Balg mit Schädel) von Tomohon (28. III 94)
1 fem. (in Spiritus) von Kottabuna an der Grenze der Minahassa (I 94)
1 fem. juv. (Balg mit Schädel) "Minahassa" (1893), weisser Fleck, der Jugendform entsprechend, schwächer,

während zwei Exemplare von Bolang Mongondo und von Buol, westlich von Gorontalo, den Fleck nicht besitzen, und zwar:

1 mas (in Spiritus) zwischen Kottabangon und Bolang Mongondo c 250 m hock (3. XII 93)

1 mas (in Spiritus) von der Nordseite der Matinangkette, c 1000 m hoch (VIII 94).

Bei dem Exemplare von Bolang Mongondo war dies Fehlen des weissen Fleckes den Sammlern schon selbst aufgefallen, indem sie auf der Etiquette bemerkten: 'leucomus var.'.

Ebenso wie die fünf Minahassa-Exemplare der Herren Sarasin verhalten sich drei Minahassa-Exemplare von Manado, Likupang und der Masarang-Kette, die das Dresdner Museum seit 1896 von der Ausbeute des Hrn. Hose erhielt. Sie zeigen alle den weissen Halsfleck gut ausgeprägt.

(Man vergleiche zur Lage der Fundorte die Sarasinschen Karten Taf. 13 Zeitschr. Ges. Erdk. Berlin 1894 und Taf. 10 ib. 1895, sowie die schon citirte Karte in den 'Birds of Celebes'.)

Es scheint mir ausgeschlossen, dass hier ein Zufall obwaltet. Das Hochplateau des Poigar bildet vielleicht im Grossen und Ganzen die Grenze der gefleckten von der ungefleckten Form, wenn westlich davon auch erstere noch vorkommen mag. Sarasins sagen (Z. Erdk. Berlin 1894, 356: 'Werfen wir hier einen kurzen Rückblick auf den von uns durchschrittenen Weg von Karoa bis ... Popo, so warden wir gewahr, dass ein Hochplateau von durchschnittlich 1000 m Höhe die Minahassa vom Nachbarreich Bolang-Mongondo scheidet. Wir wollen dasselbe das Plateau von Poigar nennen ...'

Die ungefleckte Form lässt sich nur als Subspecies von leucomus abtrennen, da Uebergänge zwischen beiden vorhanden zu sein scheinen (vgl. Abh. Ber. 1896/7 Nr. 6 S. 26); jedenfalls aber müssen weitere Exemplare vom Westen der Minahassa an nicht nur die Thatsachen erst weiter erhärten, sondern auch die genaue Umgrenzung der ungefleckten von der gefleckten Form, sowie die Umgrenzung der Uebergangsformen feststellen, ehe diese Auffassung als einwandfrei angesehen werden kann.

Es werden die anderen Formen der Leucomus-Gruppe vielleicht auch nur subspecifisch aufzufassen sein, wenn Uebergänge zwischen ihnen gefunden werden sollten. Die genaue Kenntniss von Celebes lässt eben noch ausserordentlich viel zu wünschen übrig, wir kennen dieses Land erst ganz oberflächlich und ungenügend.

Es wären nunmehr zu unterscheiden:

Sciurus leucomus Müll. Schl., von der Minahassa
Sciurus leucomus occidentalis (M.), westlich von der Minahassa bis Buol
Sciurus tonkeanus M., Nordost Celebes
Sciurus sarasinorum M., Central Celebes
Sciurus weberi Jent., West Central Celebes.
Von Südost und Südwest Celebes ist die Leucomus-Gruppe noch gänzlich unbekannt. Auch die Celebes nahe umliegenden Inseln könnten noch abweichende Formen Bergen."

APPENDIX 5

The Descriptions of *Sciurus topapuensis* and *Sciurus mowewensis* by Roux (1910: 518–519) in the Original German

"7) *Sciurus topapuensis* n. sp.

1 Balg ♀. Topapugebirge 1550 m. Central-Celebes, 16. Sept. 1902.

Das Tier steht *Sc. tonkeanus* Meyer am nächsten,-zeigt jedoch gewisse Unterschiede. Die allgemeine Färbung des Kopfes, des Rückens und des Schwanzes ist dieselbe, diejenige der Bauchseite ist aber verschieden. Statt der gewöhnlichen ziegelrötlichen Färbung zeigt sie einen graugelblichen Ton, da die Basis der Haare grau ist, die Spitze aber mehr gelblich.

Die Ohren sind mit einem sehr deutlichen Büschel versehen, der dieselbe Färbung zeigt wie der Kopf. Auf den Körperseiten und auf den Gliedmaßen ist der gelbliche Farbenton etwas heller als auf dem Rücken. Die Haare des Schwanzes haben drei breite, gelbbraune Ringe, von denen die zwei unteren etwas dunkler gefärbt sind als das dritte subterminale. Die meisten Haare des Endbüschels schwarz gefärbt und mit einem breiten gelben Terminalring versehen.

Maße: Totallänge 30, Kopflänge 5, Körper 10 cm; Schwanz mit Büschel 15, Büschel 5,5 cm; Hinterfuß mit Klaue 4,1, Vorderfuß mit Klaue 2,5, Ohr mit Büschel 1,3 cm.

Nach dem Schädel zu schließen, ist das Tier ausgewachsen. Er zeigt mit demjenigen von *Sc. leucomus* keinen Unterschied. Die Dimensionen dieser Form stehen etwas unter dem Normalen für die Arten der *Leucomus*-Gruppe. Auch die Bauchfläche ist bei allen andern Arten ziegelrot. Nur bei dieser Species ist sie grau. Ob das vielleicht nur der Jahreszeit zuzuschreiben ist, kann ich nicht beurteilen. In der Gruppe des *Sc. notatus* zeigt sich etwas ähnliches."

"10) *Sciurus mowewensis* nov. sp.

1 ♀ Mowewe. Südost-Celebes. 23. Februar 1903.

1 ♂ am Ahuafluß. Südost-Celebes. 26. Februar 1906.

Oben wurde bereits von der einzigen Species gesprochen, die man von der südöstlichen Halbinsel bis jetzt kannte. In dem neuen Sarasinschen Material fanden sich 2 Bälge, die ungefähr aus dem Centrum dieser Region, aus zwei benachbarten Fundorten herstammen. Diese Bälge sind mit *Sc. sarasinorum* sehr nahe verwandt, aber doch von ihm etwas verschieden. Die Körpergröße ist dieselbe, ebenso diejenige des Schwanzes; der Kopf ist etwas kürzer.

Die 2 Felle zeigen die gleiche Färbung. Die Haare des Rückens sind gelbbraun und schwarz geringelt; die braune Farbe ist auf der medianen Zone dunkler als auf den Seiten, wo sie einen mehr gräulichen Ton besitzt. Dasselbe habe ich auch bei *Sc. leucomus* beobachtet. Die Ohrbüschel sind sehr gut entwickelt; sie sind weiß mit einen deutlich gelblichen Anflug. Das Innere des Ohrdeckels ist mit feinen fuchsroten Härchen versehen. Um das Auge herum ist ein aus feinen und kurzen Haaren gebildeter gelbbrauner Ring zu sehen. Die seitlichen Teile der Schnauze bis fast unter das Auge sind ziegelrot. Bei *Sc. sarasinorum* zeigen sie dieselbe Färbung wie der Rest des Kopfes. Die Bauchfläche, die Unterseite der Gliedmaßen und ein Streifen der Analgegend bis zum ersten Fünftel des Schwanzes reichend, ziegelrot gefärbt. Dieselbe Koloration findet sich, etwas heller und mit Schwarz vermischt, auf der Oberseite der Füße. Der Rest der Gliedmaßen ist wie die Körperseiten graugelb und schwarz. Der Schwanz zeigt ungefähr dieselbe Färbung wie *Sc. sarasinorum*; nur ist er im ganzen nicht so schwarz, sondern mehr braun, weil die braunen Ringe breiter sind. Der subterminale Teil der Haare ist weiß; die Haare des Büschels sind auch meistens weißlich an der Spitze.

	Maße:	
	♀	♂
Totallänge	36,7 cm	36 cm
Kopflänge	5,7	6,5
Körperlänge	13	11,5
Schwanz mit Büschel	18	18
Büschel	55	70
Hinterfuß mit Klauen	41	40
Vorderfuß - -	25	26
Ohr mit Büschel	15	15

[Note: Roux apparently means mm in the last four entries]

Es ist höchst wahrscheinlich, daß die südliche Halbinsel auch *Sciurus*-Arten beherbergt, die zur *Leucomus*-Gruppe gehören Bis jetzt sind sie aber noch nicht bekannt."

APPENDIX 6

The Description of *Sciurus erythromelas* by Temminck (1853: 248–249) in the Original French

"ÉCUREUIL ÉRYTHROMÉLANE.
SCIURUS ERYTHROMELAS.

Il est heureux que nous ayons pu recevoir cet écureuil nouveau dans son pelage des noces ou à l'époque du rut, en même temps que nous sont parvenus, de la même contrée, des individus tués dans la saison opposée de l'année; obtenus séparément et capturés dans des localités différentes, nous aurions pu hésiter à les réunir sous une rubrique, tant est remarquable la différence que ces deux livrées présentent.

Dans celle de la saison du rut, la queue est pourvue de poils longs, plus ou moins distiques. Seulement deux couleurs principales revêtent le pelage; un noir très-profond et comme enduit de vernis couvre toute la tête, les parties du corps jusqu'à mi-côte, le haut des quatre membres et la queue; toutes les parties du dessous du corps, la face intérieure des jambes, une partie des flancs, et les extrémités des pieds sout d'un rouge foncé, très-vif; les moustaches prennent naissance au centre d'une petite tache grise.

Le pelage parfait dans la saison opposée à celle du rut, est peint avec plus de recherche et les teintes en sont plus variées. La queue a des poils moins longs et sa forme est arrondie. Le pelage du sommet de la tête, les parties supérieures du cou et du corps jusqu'aux flancs, de la face extérieure des membres et de la totalité de la queue, sont annelés de bandes noires, qui alternent avec d'autres plus petites et moins larges de moitié, et qui sont d'un roux-foncé; la région des yeux et des moustaches ainsi que les joues portent une teinte rouge-claire; le menton, la gorge, les parties inférieures du corps et celles intérieures des membres sont d'un roux foncé, mais terne; les extrémités des jambes sont noires; sur les flancs à mi-côte, et d'une jambe à l'autre, se voient deux bandes; la supérieure, assez étroite, est peinte d'ocre-grisâtre, l'inférieure très-large est d'un noir profond: ces bandes disparaissent vers le temps du rut; la supérieure vient se fondre dans le noir plein du dos, et l'inférieure prend la teinte rouge intense des autres parties du dessous du corps; les anneaux d'un roux foncé aux parties supérieures disparaissent par le frottement et l'usure du bout des poils.

L'on conçoit que les individus dans le passage de l'une à l'autre de ces livrées, offrent des variétés intermédiaries, qui ont plus ou moins de ressemblance avec celles de l'étât parfait, dans les deux saisons opposées de l'année.

Longueur totale de 17, 18 à 19 pouces, sur laquelle la queue prend 10 ou 9½ pouces.

Patrie. Les parties septentrionales de Célèbes, Gorontalo et Kema."

APPENDIX 7

The Description of *Sciurus erythrogenys* by Schlegel (1863: 29) in the Original French

"SCIURUS ERYTHROGENYS.

(Zoogdieren, Plaat 2, fig. 3).

Nous avons déjà fait observer, que Temminck a confoundu cette espèce avec la précédente: on doit en conséquence rapporter à celle du présent article la description des individus de son erythromelas en pelage parfait dans la saison opposée à celle du rut: *l. c.*, p. 248.

Notre écureuil à joues rousses s'éloigne de l'erythromelas par ses formes moins trapues, par sa queue plus courte et moins touffue, ainsi que par ses teintes; et il se rapproche, sous tous ces rapports, beaucoup plus du Sciurus vittatus que des autres espèces.

Longueur totale, 8 pouces. Queue, 9 pouces. Côtés de la tête, d'un roux rougeâtre clair. Dessous de la tête, du cou, du tronc, et face interne des pieds, d'un marron rougeâtre foncé bordé vers le haut, sur les côtés du ventre, d'une raie noire assez large. Les poils de toutes les autres parties sont annelés de noir et de roussâtre; mais de la sorte que cette première teinte prend le dessus sur la nuque, le dos et plus particulièrement sur les mains et les pieds de derrière en bas des jambes, tandis que les anneaux clairs dominent sur les poils bordant la raie noire des flancs, pour y former une raie claire peu large, mais apparente.

Le Sciurus erythrogenys habite, comme l'erythromelas, la pointe septentrionale de l'île de Célèbes; mais il se trouve sur la côte opposée, dans les environs de Kéma, qui nourrit plusieurs espèces d'animaux différents de ceux de Menado."

APPENDIX 8

The Account of *Sciurus leucomus* as Provided by Meyer (1896: 25–26) in the Original German in His "Säugethiere vom Celebes- und Philippinen-Archipel"

"14. Sciurus leucomus Müll. Schl.

Tafel X Figur 2 (unter 1/3 n. Gr.)

Diese Art hat bekanntlich einen grossen weisslichen Fleck jederseits am Hinterhals und auch Schwarz an den Ohren. Von dem Weiss am Halse sagt Anderson (Anat. Zool. Res. I, 252 1878): 'The series in the Leyden and Paris Museums from the Celebes prove that the white on the side of the neck is not always present, for one specimen shows it disappearing and in another there is no trace of it, and others lead from the one to the other extreme, but when this neck spot is fully developed it forms a great violet-white lappet.' Mir liegen 16 Exemplare von Main (10), Manado (1), Lotta (3) und Amurang (2) in der Minahassa, 2 von Gorontalo und 2 von der Insel Lembeh bei Kema vor. Bei manchen Weibchen ist der helle Fleck fast mehr ausgeprägt als bei den Männchen, allein dieser Character hat wie die Exemplare ergeben, Nichts mit dem Geschlechte zu thun, auch Nichts mit der Jahreszeit oder der Localität, denn Individuen z. B. vom Februar und von demselben Orte (Main) zeigen weniger gut und sehr gut ausgeprägte Flecke. Anderson constatirte nur die Thatsache des in verschiedenem Grad der Ausbildung geprägten Halsschmuckes bei verschiedenen Exemplaren, wenn in seinen Worten auch vielleicht liegt, dass er meint, der weisse Fleck variire in seiner Ausbildung individuell, und es habe der Grad der Ausbildung keinen Bezug auf einen andern Factor. Ich halte jedoch dafür, dass es en Alterscharakter ist, wenigstens hat ein kleines und, wie auch der Schädel beweist, jugendliches Exemplar von Amurang (B 622) keine Andeutung des Weiss, dagegen ein grosses und, wie der Schädel beweist, adultes von ebendaher (B 621) einen gut ausgeprägten weissen Fleck. Ebenso ist ein Exemplar von Main (B 2745) mit wenig ausgebildetem Flecke noch Jünger, wie de Zahnbeschaffenheit, die geringe Schädelgrösse und der Zustand der Schädelnähte beweisen. Ich glaube daher, dass diese Exemplare meine Auffassung begründen können. Auf der anderen Seite zeigt von den 2 Exemplaren von Gorontalo das eine (B 168) keine Spur von Weiss, und es ist nach dem Schädel ein ganz altes Individuum, und das andere (857), ebenfalls adult, hat den Fleck nur sehr schwach entwickelt. Dass die oben namhaft gemachten 2 jungen Exemplare von Amurang und Main innerhalb einer Serie von 18 (wenn wir die 2 von Gorontalo ausser Betracht lassen) nur 'zufällig' kein oder wenig Weiss haben sollten, scheint mir ausgeschlossen zu sein, und es muss daher für die Gorontaloschen nach einer anderen Erklärung gesucht werden. Es ist nun auffallend, dasse die adulten Exemplare des Leidener Museums (Jentink: Notes Leyden Mus. 1883 V, 130) von Panibi, Modelido und Limbotto bei Gorontalo (Nr. 12, 13 und 16) auch wenig oder gar kein Weiss haben, während die adulten Exemplare aus der Minahassa (Nr. 1–5) es gut entwickelt zeigen Allerdings haben die von Tulabello and Paguat in Gorontaloschen (Nr. 9–11) das Weiss sehr gut entwickelt und dieses widerspricht dem, dass der weisse Fleck im Gorontaloschen fehle. Sollte hier vielleicht eine Uebergangsform von der typischen weissfleckigen der Minahassa zu einer noch unbekannten ungefleckten südlicheren Form vorliegen, wie *Sc. Tonkeanus* vom Nordosten, aber mit Schwarz an den Ohren? In der Berührungzone zweier solcher Subspecies dürfte der betreffende Charakter mehr oder weniger ausgeprägt sein. Immerhin wird man annehmen können, dass die weissfleckige Form sich aus der ungefleckten differenzirt habe, da Junge der gefleckten noch heute ungefleckt sind, wenn auch Sicherheit über diese Frage erst durch ein grösseres Material gewonnen warden kann. Träfe meine Vermuthung nicht zu, so läge in *Sc. leucomus* eine in Bezug auf die Halsflecke noch nicht stabil gewordene, oder eine in der Abänderung begriffene Art vor.

Die zwei Exemplare von *leucomus* von der Insel Lembeh, die leicht aus den mir vorliegenden vielen Festlandexemplaren von typischen *leucomus* herauszukennen sind, zeigen eine mehr ins Braune spielende Färbung. Es scheint dieser Unterschied jedoch zu geringfügig und durch zu wenig Exemplare als constant belegt, um eine Abtrennung zu rechtfertigen."